Pedobiologia **24**, 255—296 (1982)

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Collembola in Norwegian coniferous forest soils
I. Relations to plant communities and soil fertility

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With 14 figures

(Accepted: 82-06-18)

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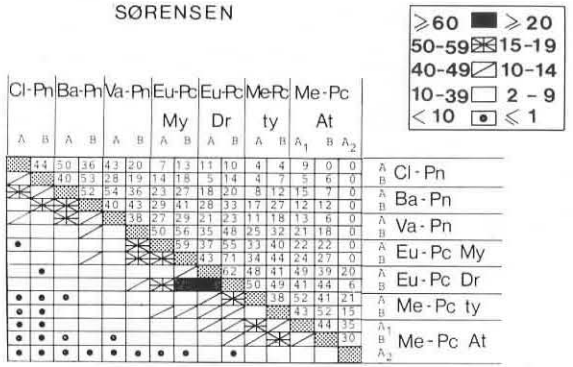
1. Introduction

Collembola are among the dominant soil animals in northern coniferous forests. Their role in soil processes is yet poorly understood. However, their high abundance throughout the organic layers in the soil indicates that they take part in many phases of decomposition.

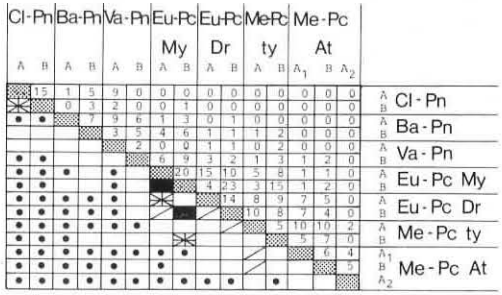
A better understanding of the function of these animals in forest systems must be based on knowledge of their abundance and species composition in different soils and plant communities, as well as their vertical distribution and relations to soil chemistry. The present paper is part of an investigation which will enlighten these aspects in the main types of Norwegian coniferous forest habitats. The soils vary from very poor iron podzols to fertile brown earth (from Typic Udipsamment to Aquic Haploboroll, USDA classification).

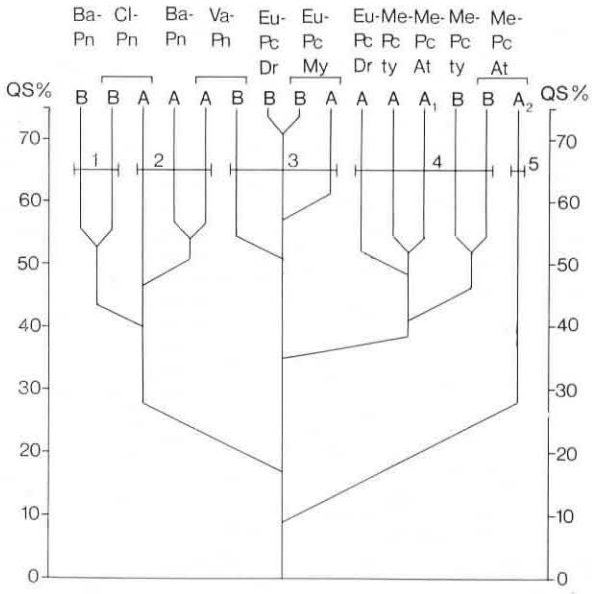
One of the early studies of Collembola in different coniferous forest habitats in Scandinavia was made by Forsslund (1944). However, the number of samples per habitat was small. Furthermore, more efficient extraction methods have been developed since then, and the systematics of many species have changed. Interest in the study of Collembola has in-

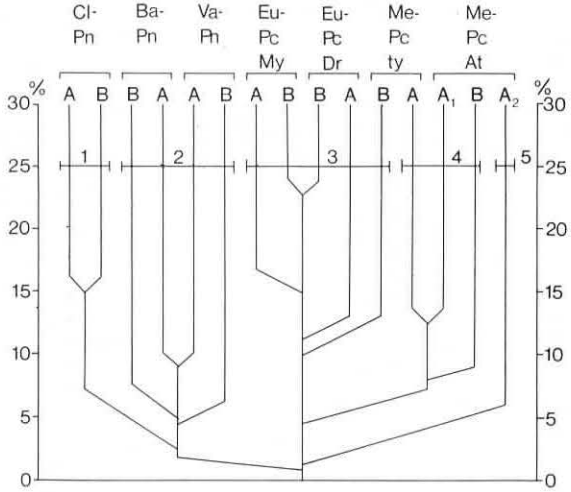
SØRENSEN



SPATZ







creased during the past two decades in Scandinavia. Many of the studies from coniferous forest soil have, however, been restricted to one forest type (AXELSSON *et al.* 1973, POOLE 1964, PERSSON 1975, WIRÉN 1975, HUHTA 1976, LEINAAS 1976, LOHM *et al.* 1977, BENGTSSON & RUNDGREN 1980, BÅÅTH *et al.* 1980). Among the studies covering more than one coniferous forest habitat, only the total number of Collembola have been noted in some cases (HUHTA *et al.* 1967, 1969, HUTHA & KOSKENNIEMI 1975, HUHTA 1976). If two or more habitats have been compared, the samplings have not been made quantitatively (PALISSA 1966, BÖDVARSSON 1973).

While the present paper focuses upon the relationship between the Collembola fauna and different plant communities, a second will deal with the vertical zonation in the soil, and a third with relations to soil chemical properties.

2. Description of habitats

2.1. General

Two study areas were chosen not far from Oslo, one in the lowland and one at higher altitudes inland. Eight habitats within the lowland locality (A) and seven habitats within the other locality (B) were selected for sampling.

The habitats in each area ranged from low productive, nutrient poor, acid podzolic soils with raw humus, to highly productive, nutritious brown earth with mull formation. Since there is a correlation between soil properties and the ground cover vegetation in coniferous forest (e.g. DAHL *et al.* 1967), the habitats were selected on the basis of phytosociological criteria. Some habitats were identical to those earlier used by ABRAHAMSEN (1972) during similar studies on Enchytraeidae.

2.2. Localization and climate

Study area A is situated near Ås, about 30 km south of Oslo. Area B is located in Skrukkelia, NW of lake Hurdalssjøen, about 60 km north of Oslo. Maps of the areas have been presented by ABRAHAMSEN (1972, Fig. 1). However, not all of his original sample plots were found to be intact. In the present study, his habitats no. 5 and 6 near Lake Årungen were used in aerea A, and his habitats no. 1—4 in area B. The other habitats were selected within a few kilo-meters from these.

Temperature and precipitation data from the two areas were presented by ABRAHAMSEN (1972). Mean annual air temperature is 5.5 °C in area A and 2.8 °C in area B. Mean yearly precipitation is 866 mm in area A, and the number of days with snow-cover is 130. For area B, better estimations of precipitation exist today than those given by ABRAHAMSEN (1972). Mean yearly precipitation is 990 mm, and the number of days with snow-cover is 183. Clearly, area B is colder, has a longer winter period and slightly more precipitation than area A.

2.3. Topography, rocks and soils

The terrain in study area A is rather flat, while area B is hilly with variations in altitude of 400 m within a few km. The altitude of each habitat is given in Table 1. Rocks of gneiss predominate in area A, while plutonic rocks with syenite are typical for area B. The first area often has a cover of marine sediments, as it was situated below the marine limit during the last glaciation. In the second area, the soil is mainly moranic deposits, but glacifluvial sediments occur in the floor of the valleys. The soil profile and humus type of each sampling plot appear in Table 1, together with information on pH, loss on ignition and nitrogen content in the upper 0—3 and 3—6 cm layers. A more complete chemical description of the soils will appear in a later paper, when direct relationships between soil chemistry and Collembola are discussed.

2.4. Vegetation

2.4.1. The vegetation types

The vegetation types in coniferous forests in South Norway have been described by KIELLAND-LUND (1962, 1965, 1967a, b, 1973, 1981). In the present work, the Collembola fauna has been investigated in soils from seven different vegetation types. The system and abbreviations used have

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Fig. 1. Floristic similarity between the various vegetation types in the two study areas (A and B). In the lower half, the sample plots have been classified into natural groups. Information on the different vegetation types and the two indexes applied (SØRENSEN & SPATZ) is given in the text.

Table 1. Some main properties of the investigated habitats, together with average sampling depth

Plant community Study area	Cl-Pn		Ba-Pn		Va-Pn	
	A*)	B*)	A	B	A*)	B
Soil profile	Iron podzol		Shallow peat	Iron podzol		
Humus type	Raw humus (crust)		Peat	Raw humus (felty)		
Thickness of raw humus layer (cm)	1.5	1.5		5.2	4.5	5.9
Soil pH						
0—3 cm	3.74	3.70	3.65	3.79	3.85	3.98
3—6 cm	3.76	3.83	3.42	3.55	3.62	3.59
Loss on ignition (%)						
0—3 cm	71.8	51.3	95.3	92.5	78.9	72.7
3—6 cm	27.6	14.4	79.1	50.0	79.8	16.9
N in % of loss on ignition						
0—3 cm	1.84	1.45	1.49	1.30	1.58	2.23
3—6 cm	2.23	2.19	1.52	1.41	0.77	2.07
Average depth of soil samples (cm)	3.8	4.3	10.4	9.9	11.5	10.0
Dominant tree species	*Pinus sylvestris*	(Open area)	*Pinus sylvestris*	*Picea abies* (scarce)	*Pinus sylvestris*	*Betula pubescens*
Age of forest	160	(Open area)	160	220 (one tree)	160	60 *(Picea abies)*
Height above sea level (m)	140	530	140	530	100	330
Size of plot (m^2)	10	3 (patches)	10	5	15	25

Note: Raw humus types are according to DUMANSKI (1978).

been summarized by DAHL *et al.* (1967). Listed after increasing fertility of the soil, the vegetation types investigated were as follows:

1. Association Cladonio-Pinetum **(Cl-Pn)**
2. Association Barbilophozio-Pinetum **(Ba-Pn)**
3. Association Vaccinio-Pinetum **(Va-Pn)**
4. Association Eu-Piceetum
4.1. *Myrtillus* subassociation **(Eu-Pc My)**
4.2. *Dryopteris* subassociation **(Eu-Pc Dr)**
5. Association Melico-Piceetum
5.1. Typical subassociation **(Me-Pc ty)**
5.2. *Athyrium* subassociation **(Me-Pc At).**

In the present investigation, one vegetation type is missing, as it was absent in the two study areas. This is the association Vaccinio uliginosi-Pinetum (Vu-Pn), which is among the poorest in the system. In area A, two habitats of the most fertile type were investigated. One of these (A_2), was unusually fertile, and had a comparatively high soil pH (Table 1). The vegetation was also different in these two habitats.

Complete flora lists for the fifteen investigated sites are shown in Table 2. The nomenclature is according to LID (1974) (vascular plants), DAHL & KROG (1973) (lichens), NYHOLM (1954—1969) (musci), and ARNELL (1956) (hepaticae). The degree of cover for each species is given according to BRAUN-BLANQUET's scale: (+) single specimens only; (1) 5% cover, and few specimens; (2) 5—25% cover, and many specimens; (3) 25—50% cover; (4) 50—75% cover; (5) 75—100% cover. During

Eu-Pc My		Eu-Pc Dr		Me-Pc ty		Me-Pc At		
A*)	B	A	B	A	B	A_1*)	B	A_2
⟨	⟩	Brown earth	Iron podzol	Brown earth		⟨		⟩
⟨	⟩			Mull	Raw humus (granular)	Mull	⟨	⟩
4.0	6.5	4.5	6.6		15.0			
3.65	3.79	4.18	4.20	4.35	5.22	4.16	5.58	5.88
3.32	3.44	3.90	3.73	3.89	5.21	4.10	5.54	6.09
79.7	91.1	49.6	80.0	77.0	67.4	19.3	79.7	11.2
25.0	45.1	23.7	25.5	29.0	58.6	12.6	56.9	11.5
2.18	1.61	2.21	1.79	1.95	2.41	3.04	2.49	2.98
2.00	1.32	3.14	1.76	2.88	2.73	3.34	3.40	2.24
12.0	11.9	12.0	10.3	12.0	12.0	12.0	11.1	11.7
Picea abies								*Fraxinus excelsior*
100	110	60	110	60	50	60	50	60 *(Picea abies)*
120	500	70	330	50	400	50	400	60
10	25	6	25	25	10	25	10	25

*) Horizon weakly developed

the analysis, distinctions were made between tree-, shrub-, field- and moss layers. The descriptions are based upon 4—5 quadrat of 1 m². In the Cl-Pn habitat in area B, however, the quadrat were 0.25 m² due to the patchy distribution of this vegetation type. In four habitats (Me-Pc ty in area A and Va-Pn, Eu-Pc My and Eu-Pc Dr in area B), ABRAHAMSEN's (1972) data have been used, as the vegetation had probably not changed during the last decade.

The size of each sample plot, the age of the forest, and the dominant tree species are listed for each habitat in Table 1.

Cl-Pn was characterized by a dense cover of *Cladonia*-species. In Ba-Pn, the cover of these lichens was reduced, and *Calluna vulgaris* was common in the field layer. Va-Pn differed from the two former types by a dense cover of *Vaccinium myrtillus* or *Vaccinium vitis-idaea* and the absence of *Calluna vulgaris*, while the presence of certain lichens distinguished it from the spruce forest communities. In spruce forest, *Vaccinium myrtillus* dominated the Eu-Pc My. In addition to the absence of lichens, this vegetation type differed from Va-Pn by the presence of *Luzula pilosa*, *Sorbus aucuparia* and by a fairly good cover of *Deschampsia flexuosa* and *Maianthemum bifolium*. Eu-Pc Dr was characterized by *Thelypteris phegopteris* and *Dryopteris dilatata*. In addition, the presence of *Anemone nemorosa* and *Oxalis acetocella* distinguished it from Eu-Pc My. Me-Pc ty differed from Eu-Pc Dr by the presence of *Carex digitata*, *Melampyrum sylvaticum*, *Viola riviniana* and *Fragaria vesca*. Characteristic species for Me-Pc At (the tall herb spruce forest) were *Filipendula ulmaria*, *Athyrium felix-femina* and *Aconitum septentrionalis*.

Some comments should be made about three of the habitats in locality A. The Eu-Pc Dr habitat was probably influenced by grazing, but this was the only site in area A where this vegetation type could be found. In the first Me-Pc At habitat (A_1), the forest was cut during the winter of 1977/78. When the

Table 2. Complete flora list for the investigated habitats. The symbols for the degree of cover are according to BRAUN-BLANQUET's scale (see text).

Type:	Cl - Pn		Ba - Pn		Va - Pn		Eu - Pc My		Eu - Pc Dr		Me - Pc ty		Me - Pc At		
Area:	A	B	A	B	A	B	A	B	A	B	A	B	A_1	B	A_2
Tree layer															
Picea abies				1			5	2	5	2	4	2		1	
Pinus silvestris	1		4		4										
Betula pubescens						4								1	
Fraxinus excelsior															4
Shrub layer															
Sorbus aucuparia						+		1		1	1			+	
Picea abies								2		+		1			
Betula pubescens		+						+		+					
Pinus silvestris			+		1										
Populus tremula					+										
Salix sp.						+							+		
Fraxinus excelsior															2
Quercus robur											+				
Field layer															
Calluna vulgaris	+	+	4	2											
Vaccinium uliginosum		+		2											
Empetrum hermaphroditum		1		3											
Pinus silvestris	+				+										
Vaccinium myrtillus		+	2	2	1	3	3	4	3	2	+	1	+	+	
V. vitis - idaea		+	1	1	3	1	1	1		+		2		+	
Deschampsia flexuosa				+	+	+	2	1	2	2	+	1			
Maianthemum bifolium						+	2	1	2	1	+	1	+	+	
Trientalis europaea						+	1	+		+		+		+	
Linnea borealis						+	+	+		1		+			
Luzula pilosa								+	1	1	+	+	+	+	
Gymnocarpium dryopteris								+	2	3	1		1	+	
Sorbus aucuparia							+	+				+			
Picea abies							+		+	+		+	+	+	
Lycopodium annotinum							+			+	+			+	
Melampyrum pratense								+		+					
Carex sp.							+								
Oxalis acetosella									1	+	5	+	1	2	1
Anemone nemorosa									+	1	+	1	1	+	
Thelypteris phegopteris									2	1	+			2	
Dryopteris dilatata									1	+	+			+	
Athyrium filix-femina									+				+		+
Galeopsis tetrahit									+						1
Anthoxanthum odoratum									+						
Stellaria graminea									+						
Carex digitata											1	+	+		
Melampyrum sylvaticum											+	1		+	
Viola riviniana											+	+	+		+
Veronica officinalis												+	+	+	
Agrostis tenuis											+	1	+		
Rubus idaeus											+		2	1	+
R. saxatilis												2		+	
Fragaria vesca												+		+	
Deschampsia caespitosa												1		2	
Aconitum septentrionale												+		1	
Equisetum sylvaticum											+		2	+	
Utilium effusum											+		1		+
Geranium sylvaticum												1		+	
Antriscus sylvestris											+				+
Pyrola rotundifolia												1			
Dryopteris carthusiana											+		+		
Solidago virgaurea											+				
Potentilla repens												+			
Galeopsis bifida											+				
Carex pilulifera											+				
C. pallescens												+			
Filipendula ulmaria														3	2
Valeriana sambucifolia														2	+
Stellaria nemorum													2		1
Pteridium aquilinum													+		1
Gnaphalium sylvaticum													+		
Galium palustre														+	+
Tussilago farfara														2	
Viola palustris														1	
Geum rivale														1	
Hieracium sp.														+	
Alchemilla sp.														+	
Ranunculus repens															2
Lactuca muralis															1
Equisetum pratense															1
Hepatica nobilis															+
Trollius europaeus															+
Melica nutans															+
Impatiens noli-tangere															+
Actaea spicata															+
Urtica dioica															+
Cirsium palustre															+
Taraxacum sp.															+
Fraxinus excelsior															+
Senecio vulgaris															+

Table 2 (continued)

Type:	Cl - Pn		Ba - Pn		Va - Pn		Eu - Pc My		Eu - Pc Dr		Me - Pc ty		Me - Pc At		
Area:	A	B	A	B	A	B	A	B	A	B	A	B	A_1	B	A_2
Moss layer															
Dicranum fuscescens	+	1		2											
Pohlia nutans	+	+													
Aulacomnium palustre	1														
Orthodicranum montanum		+													
Sphagnum nemoreum			2	+											
Polytrichum juniperinum				+		+									
Ptilidium ciliare				+	+							+			
Orthocaulis floerkii				1											
Pleurozium schreberi	+		1	2	+	1	2	2	3	+	+	3	+		
Dicranum rugosum	1		4	1	+	2		1	+	+			+		
D. scoparium						1	3		+	+	+	1			
Hylocomium splendens				+		+		2	1	2	1	1			
Barbilophozia lycopodioides				+				1		1		2		+	
Ptilium crista-castrensis							+			3	+		+		
Polytrichum formosum							1	1			+				
Rhytidadelphus squarrosus									2	+		1	+	1	+
Dicranum majus										1	+		1	+	
Plagiochila major									+		+	+	+	+	+
Mnium affine									+		1		+	2	+
Hylocomium umbratum									+					1	
Sphagnum girgensohnii										1					
Polytrichum commune										+					
Cirriphyllum piliferum												+	1	2	2
Rhytidadelphus triquetrus												1		+	+
Brachythecium starkei											2				
B. reflexum											+			+	+
Rhodobryum roseum												+	+	+	
Plagiothecium denticulatum												+		+	
P. laetum											2				
Brachythecium salebrosum												+			
Rhytidiadelphus calvescens											+				
Dolichotheca seligeri											+				
Lophocolea heterophylla											+				
Bryum sp.												+			
Peltigera canina												+			
Atrichum undulatum													+	+	+
Brachythecium rutabulum														+	+
Mnium cinclidioides														+	
M. punctatum														+	
Sphagnum squarrosum														+	
Mnium undulatum															1
Eurhynchium praelongum															+
Drepanocladus sp.															+
Cladonia silvatica coll.	4	3	+	2	+										
Cl. rangiferina	1	3	+	1		+									
Cl. alpestris	2														
Cetraria islandica		1		2											
Cladonia chlorophaea	+	+			+										
Cl. gracilis					1	+									
Cl. uncialis	+														
Cl. coniocraea		+													
Cl. bacillaris					+										
Cl. cenotea					+										
Cl. crispata						+									
Cl. sp.				+											
Number of species	12	14	9	20	13	17	14	17	22	27	39	38	30	46	36

vegetation analysis was made in spring 1978, the moss cover had been somewhat reduced due to increased light and dryness. The second Me-Pc At habitat (A_2) was atypic in some respects, but it was included since it belonged to the very richest soils which can be found in Norwegian coniferous forests. The spruce trees on that plot were cut 4—5 years before the sampling, and a rather dense stand of *Fraxinus excelsior* had grown up. Some of the field layer plants were more typical for deciduous forest than for spruce forest (e.g. *Stellaria nemorum*, *Ranunculus repens*, *Impatiens noli-tangere*). Furthermore, a brook close to the site obviously supplied the soil with nutrients carried from agricultural areas, especially during the spring flood. The brook has also probably brought seeds from plants typical for cultured soil: *Senecio vulgaris*, *Galeopsis bifida* and *Urtica dioica*.

When soils are selected by vegetation characteristics, the choice is based on the presence or absence of a limited number of "indicator" species. Even within a given area, however, the species occurring together with a certain set of indicator species may vary, and the vegetation types also merge into one other. In different localities, the same indicator species may be associated with rather different communities, due to differences in climate, geology etc. Therefore, the similarity in the total flora composition was not always greatest between habitats with the same vegetation type, but was often greater between different vegetation types in the same study area.

2.4.2. Floristic similarity

The floristic similarity between the fifteen sample plots was calculated in two ways, both by SØRENSEN's index (SØRENSEN 1948) and by the SPATZ index (MUELLER-DOMBOIS & ELLENBERG 1974).

The widely used index of SØRENSEN is $QS = \frac{2j}{a + b}$, where a and b are the number of species in the two localities and j is the number of species in common. The maximum index value is 1, but the values are commonly multiplied by 100. The limitation of this index is that it is based only on the presence or absence of each species and neglects differences in dominance or abundance. The index of SPATZ, however, takes into account the quantitative differences between two plant communities. It is written as follows: $IS = R \frac{Mc}{Ma + Mb + Mc} 100$. If we base our calculations on dominance data, the component R is achieved in the following way: for each species common to the two habitats, the smaller dominance value is divided by the greater dominance value; the resulting fractions, whose number is equal to the number of common species, are added up and the sum is divided by the total number of species in the two habitats. Mc is the sum of the dominance values in both habitats for all common species. Ma and Mb are the sum of the dominance values for species occurring only in the one, or only in the other habitat, respectively. Maximum index value is 100.

A limitation of the index is that species number is not taken directly into account. The formula is based on sums of quantitative values from different species groups. Therefore, two sites may get a high common value even if one site contains, for instance, a high number of rare species which are not shared by the other site. In conclusion, the two indexes stress different properties of the communities, and it is valuable to use both when comparisons are made.

Because the data on vegetation cover contained a category not indicated by a figure (+), this category was given the value of one, and the other categories a value of one above the registered value, before the SPATZ index was calculated.

The floristic similarity between the different sample plots expressed by SØRENSEN's and SPATZ' indices are shown in the upper part of Fig. 1. All numbers have been adjusted to the nearest whole value. The SPATZ index values are generally lower than those of SØRENSEN, because differences in the degree of cover play a great role in addition to the commonness of species. Both indexes stress the influence of local effects on the flora accompanying the "indicator" species. Thus, by SØRENSEN's index, only two sample plots showed greatest similarity to the same vegetation type in the other study area. In all other sample plots, the vegetation was most similar to a neighbouring vegetation type within the same study area. By the index of SPATZ, a higher number of plots (five) showed the highest degree of similarity with the same vegetation type in the other study area. However, concerning the other sites, the similarity was not always highest between neighbouring habitats on the scale.

In Fig. 1, lower part, the sample plots have been grouped in the way proposed by SØRENSEN (1948). Both indexes result in five main groups of sample plots, representing different levels of soil fertility. The last category consists of only one plot (A_2), which is the very rich Me-Pc At habitat, possessing a flora very different from all other plots. In general, SPATZ' index grouped the habitats better according to vegetation types than SØRENSEN's index.

3. Material and methods

3.1. Sampling

From each habitat, samples were taken twice: in spring, just after snow melt, and in autumn. In this way it was hoped to include species with different life cycle patterns and to get a representative picture of the species composition. It was also the intention to compare the fauna quantitatively and qualitatively in all habitats simultaneously. The actual collecting dates are listed in Table 3. Area B was sampled somewhat later than area A, due to later snow melt. Most samples were taken in autumn 1977 and in spring 1978.

Table 3. Sampling dates in the different habitats

	Area A								Area B
Habitat	Cl-Pn	Ba-Pn	Va-Pn	Eu-Pc My	Eu-Pc Dr	Me-Pc ty	Me-Pc At (A_1)	Me-Pc At (A_2)	All habitats:
Autumn	23. 8. 1977	23. 8. 1977	30. 8. 1977	16. 8. 1977	12. 9. 1978	10. 8. 1977	11. 8. 1977	16. 8. 1977	6.—7. 9. 1977
Spring	3. 5. 1978	3. 5. 1978	9. 5. 1978	5. 5. 1978	29. 5. 1978	5. 5. 1977	8. 5. 1978	8. 5. 1978	31. 5. to 1. 6. 1978

The abundance estimates for aggregated soil animals like Collembola depend both on sample size and sample numbers. Because counting and identification are very time-consuming, it is important to design the sampling so that relatively good estimates can be achieved on the basis of a limited number of animals. A general rule is that it is better to take many small samples than a few large ones (ABRAHAMSEN 1969, BERTHET 1971). However, according to ABRAHAMSEN (1969), the mean number of animals per soil core should not be below 10. In earlier studies from coniferous forest soils in Norway, abundance values for Collembola ranged from about 30,000 to about 150,000 m^{-2} (LEINAAS 1976, HÅGVAR & ABRAHAMSEN 1977). On this base, a soil corer covering 10 cm^2 was chosen, as it would give an estimated number of 30—150 Collembola per sample. These estimates of population densities proved to be good, and at least the most abundant species were collected in satisfactory numbers. A total of 20 soil cores were taken at each sampling in a given site, a rather high number compared with most earlier studies on Collembola. For practical reasons, this number could not be increased.

If the soil corer was not stopped by rock or stones, the samples were taken down to a depth of 12 cm. The average sampling depth appears in Table 1. One exception from this sampling pattern was the spring sample in Me-Pc ty, area A. Because the trees in this site were cut just before the planned spring sampling in 1978, material collected one year earlier had to be used. This consisted of 11 samples of 33 cm^2 down to 9 cm depth. To reduce the compression of the sample when the soil corer was inserted into the soil, the lower part of the corer was slightly conical, allowing the sample to move with only small resistance within the cylinder. The soil core was pushed gently out of the cylinder with a piston and at once divided into 3 cm thick sections. These were transported and stored in PVC rings, with both ends tightly covered by a cotton cloth. Moss or lichens were included in the upper section. If the moss layer was not very dense, the plants were gently pressed against the litter.

3.2. Storage and extraction

The samples were stored for maximum four weeks at 2—4 °C before extraction. These storage conditions are acceptable for Collembola (LEINAAS 1978a). Extraction was performed in a high gradient apparature according to MACFADYEN (1961). Fig. 2 shows the temperatures in the upper and lower surface of a raw humus sample (Eu-Pc My, 0—3 cm) during the extraction, which lasted one week. Most of the time, temperatures in the upper surface were between 30 and 35 °C, with a gradient of approximately 10 °C through the sample. At the end of the extraction, temperatures exceeded 60 °C in the top and 40 °C in the bottom. LEINAAS (1978a) showed that the temperature levels in the sample, and thereby the extraction speed, influenced the extraction efficiency of Collembola from raw humus. The temperatures in Fig. 2 are most of the time lower than those recommended by LEINAAS (1978a), which should indicate a somewhat reduced extraction efficiency in the present case.

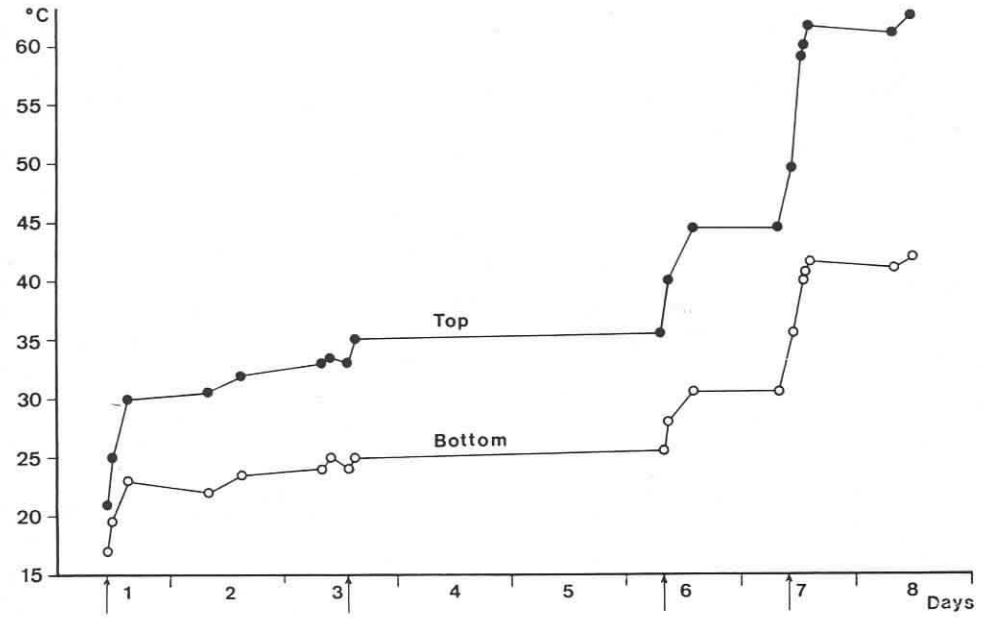


Fig. 2. Temperature in the top and bottom of a 3 cm thick soil sample during extraction (from a raw humus sample in Eu-Pc My).

As optimum heating may vary with physical and thermal properties of the soil, and also with the microclimate to which the animals are adapted, there is an unknown bias for the extraction efficiency in the other soils in this study. PETERSEN (1978a) tried to evaluate the extraction efficiency in a high gradient apparature and indicated values between 80 and 90% for Collembola. Differences were demonstrated between Collembola species, but not between size classes within species.

LEINAAS (1978b) showed that larger numbers of Collembola were extracted from frozen soil than from unfrozen soil sampled just before the onset of winter. No reproduction could have occurred in this period. He explained the difference partly by loss of animals during the slight compression of unfrozen soil, and partly by possible differences in the physiological state of the animals. For instance, in unfrozen soil, many animals may be inactive during moulting while moulting may cease during winter.

Clearly, various errors are connected with the present population data. However, because of the standardization of the methods, the material should allow for general comparisons between habitats and species.

The animals were caught in saturated picric acid, which was afterwards added 96% alcohol to about 70% for conservation. Floating animals were pushed down with a fine brush after adding a few drops of butanol (n-butyl alcohol) and heating to 60 °C. Then a small amount of glycerol was added, and the alcohol was evaporated. The remaining mixture of glycerol and picric acid was well suited for storage and counting.

3.3. Counting and identification

All collected animals were counted, mainly under 40—80× magnification. Several species could be identified directly in the vial, but a considerable part of the material needed higher magnification. These animals were embedded in Hoyer's medium, warmed and cleared, and then studied under interference contrast microscope at magnifications up to 1,000×. The small Tullberginae, which represented a large fraction of the material in all sampling sites, were first counted collectively. These animals were mainly *Tullbergia krausbaueri* BÖRNER *s.l.* However, according to recent systematics, this name covers several species, of which five were found in the present study (genus *Mesaphorura*). Also two other small Tullberginae species were recorded: *Karlstejnia norvegica* FJELLBERG and *Wankeliella mediochaeta* RUSEK. As it is a laborious work to identify large numbers of these Tullberginae, about 60 random specimens were picked out for identification from each vertical layer at each sampling in a given site. The abundance and dominance of the seven species in question were estimated from these sub-samples. If the total number of animals was less than 60, all were identified. The use of sub-samples implied that data for standard deviation and constancy (frequency) could not be achieved for these species.

The total number of Collembola collected was about 26,000 in area A and about 20,000 in area B.

3.4. Taxonomical remarks

In the present paper, the genus name *Mesaphorura* BÖRNER is used for the species which earlier were collectively named "*Tullbergia krausbaueri*". According to RUSEK's revisions of the *T. krausbaueri*-complex, my material contained the following species: *M. yosii* RUSEK, 1967, *M. sylvatica* RUSEK, 1971, *M. italica* RUSEK, 1971, *M. tenuisensillata* RUSEK, 1974, and *M. macrochaeta* RUSEK, 1976. The identifications have been checked by RUSEK.

The juvenile stages of the *Mesaphorura* species presented some difficulties. By studying animals in ecdysis, showing the characters of both the old and the new cuticula, FJELLBERG (1980, Fig. 152a) was able to identify a pre-adult stage of *M. tenuisensillata*, which has different chaetotaxi from the adults. Later, I could identify a still earlier stage of this species by the same technique. The chaetotaxi on abd. IV—V of these two juvenile stages have been depicted schematically in Fig. 3, together with a specimen in ecdysis which contains the characters of both stages. Already the youngest of these stages has two pseudocelli on each side of thorax III, as in the adult *M. tenuisensillata*. Among animals with adult chaetotaxi, the smallest specimens had no visible genital opening. This indicates that reproductive animals have moulted at least three times. In Fig. 4, the size distribution of the four mentioned development stages of this species is shown.

After the treatment of the present material, RUSEK (1980) described the juvenile stages of *M. yosii* and *M. sylvatica*. In these species, the first instar proved to have the same chaetotaxi on abd. IV—V as the youngest stage which I noted in *M. tenuisensillata* (Fig. 3, A). This indicates that the two stages depicted in Fig. 3 represent the two first instars of *M. tenuisensillata*. However, in *M. yosii* and *M. sylvatica*, the adult chaetotaxi is achieved already in the second instar (RUSEK 1980). As the identification of the early stage (A) of *M. tenuisensillata* was currently made on base of the chaetotaxi on abd. IV—V, this category would also include the first instar of other *Mesaphorura* species. This leads to an overestimation of *M. tenuisensillata* and an underestimation of other *Mesaphorura*-species in the present material. However, this discrepancy is probably not large. Stage "A" represented less than 10% of the whole *M. tenuisensillata*-material, and a large fraction of the uncertain animals were probably *M. tenuisensillata*. Adult *M. tenuisensillata* was present in all samples, very often being the dominant *Mesaphorura* species. In the spring sampling of the Cl-Pn habitat in area A, where the abundance of *M. tenuisensillata* was extremely high, there were no doubtful animals among the studied specimens.

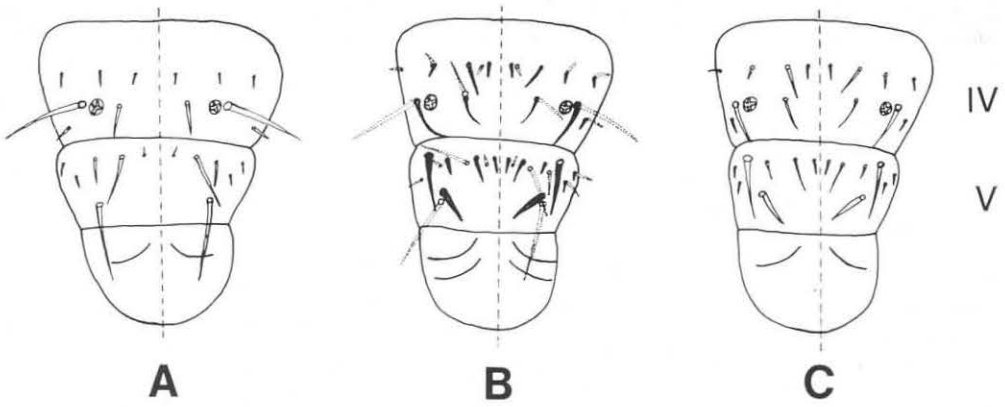


Fig. 3. Schematic presentation of the chaetotaxi on abd. IV and V in two juvenile stages of *Mesaphorura tenuisensillata*. A = an early stage (first stage?), C = pre-adult chaetotaxi, and B is an animal in ecdysis showing the characters of both A and C (stippled hairs are from the old cuticula).

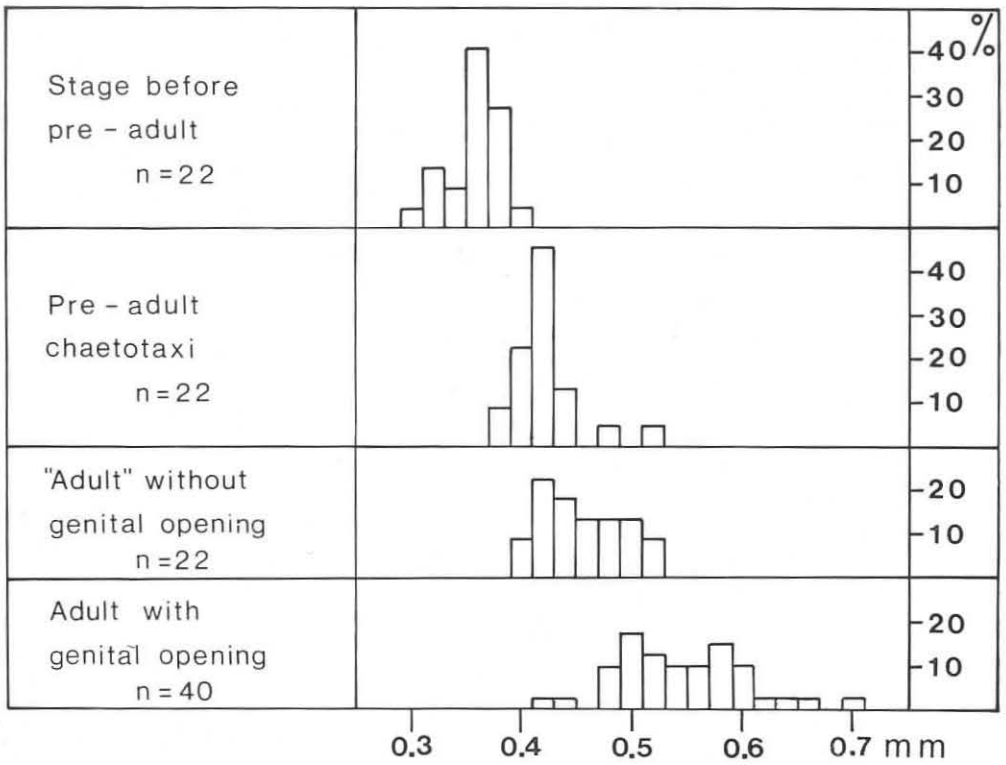


Fig. 4. Body length of *Mesaphorura tenuisensillata* specimens in different developmental stages, based on chaetotaxi and the appearance of a genital plate (see Figure 3).

Table 4. Quantitative information on the most common Collembola species (with abundance ≥ which is the percentage of soil cores in which the species was present. + indicates abundance

Vegetation type		Cl-Pn		Ba-Pn		Va-Pn	
Study area		A	B	A	B	A	B
Spring-autumn		s-a	s-a	s-a	s-a	s-a	s-a
Xenylla boerneri Axelson	Abu		21.5				
	Con		15				
Isotoma sensibilis (Tullberg)	Abu	2.4- 3.2	0.1				
	Con	45- 40	5				
Anurophorus septentrionalis Palissa	Abu	5.9-13.2	0.3- 0.2	3.6- 5.4			
	Con	90- 90	25- 15	75- 95			
Hypogastrura inermis (Tullberg)	Abu	0.5- 1.3		0.4		1.6- 1.1	
	Con	35- 70		20		63- 40	
Mesaphorura yosii Rusek	Abu	0.1	1.9- 1.5	1.6- 2.4	8.3-18.5	4.5- 5.7	7.8-11.4
	Con						
Folsomia sensibilis Kseneman	Abu	0.1	0.3- 0.2		1.3- 3.4		0.1- 0.1
	Con	5	5- 15		60- 85		5- 6
Mesaphorura sylvatica Rusek	Abu	0.1				4.2- 2.9	1.1- 0.3
	Con						
Folsomia quadrioculata (Tullberg) s.l.	Abu	10.4- 3.6	12.4- 3.0		9.3- 6.8	17.2-23.6	17.1-10.6
	Con	65- 30	95- 65		100- 95	100-100	90- 88
Anurida pygmaea (Börner)	Abu	0.4- 0.2	0.5- 0.3	2.0- 1.4	0.7- 2.6	8.6- 9.0	1.5- 1.0
	Con	20- 10	35- 15	55- 35	30- 45	100- 90	45- 53
Anurida forsslundi (Gisin)	Abu	1.1- 0.5	0.1- 0.2	3.7- 0.7	0.2- 0.4	3.6- 3.3	1.8- 2.4
	Con	50- 20	10- 15	75- 25	15- 25	84- 70	75- 82
Friesea mirabilis (Tullberg)	Abu	4.9- 6.4	6.5- 4.0	5.7- 6.0	6.2- 6.8	1.2- 2.6	3.6- 6.2
	Con	85- 65	80- 80	90- 90	95- 95	58- 55	90-100
Isotoma notabilis Schäffer	Abu	0.1	0.3- 0.2	0.1	2.5- 2.4		0.7- 0.6
	Con	5	15- 15	5	75- 65		45- 47
Willemia anophthalma Börner	Abu	0.1	0.1		0.9- 5.7	0.6- 0.2	0.5- 0.3
	Con	5	5		55- 60	21- 15	30- 29
Onychiurus absoloni (Börner)	Abu	0.4- 0.5	0.4- 0.3		0.2- 1.6	0.1	0.4- 0.2
	Con	20- 15	30- 20		5- 30	5	20- 18
Onychiurus armatus (Tullberg) s.l.	Abu	16.2- 9.9	0.9- 0.9	13.9-13.3	0.2- 1.7	6.6-15.8	7.5-15.7
	Con	100- 60	40- 40	100-100	10- 65	89-100	95-100
Lepidocyrtus lignorum (Fabricius)	Abu	1.9- 0.1	1.1- 0.1	6.4- 0.5	1.6	1.6- 0.7	0.5- 0.5
	Con	5- 5	45- 5	65- 40	65	47- 40	30- 24
Isotomiella minor (Schäffer)	Abu	1.1- 0.8	2.4- 1.2	0.2- 0.2	3.8- 7.7	8.7- 3.2	24.5-12.9
	Con	20- 25	55- 35	15- 10	85- 95	79- 65	100-100
Mesaphorura tenuisensillata Rusek	Abu	63.4- 6.4	4.4- 9.6	11.1- 0.4	1.2- 6.6	10.9- 8.3	4.6- 4.3
	Con						
Anurophorus binoculatus (Kseneman)	Abu		0.1- 0.9	0.1	3.8- 3.2	0.2	1.0- 3.1
	Con		5- 15	5	70- 80	5	30- 47
Isotoma olivacea Tullberg	Abu		0.1- 0.5	0.1- 2.4	1.1		
	Con		5- 25	5- 40	25		
Karlstejnia norvegica Fjellberg	Abu		0.1		0.1- 0.1	0.2- 1.0	0.1- 0.1
	Con						
Neelus minimus Willem	Abu		0.1- 0.1	0.1	0.1- 0.3		
	Con		10- 5	5	5- 30		
Lepidocyrtus cyaneus Tullberg	Abu			0.1- 0.4		0.1- 0.1	
	Con			5- 25		5- 10	
Isotoma viridis Bourlet	Abu				0.1- 0.2		0.1- 0.5
	Con				5- 10		10- 29
Tullbergia callipygos Börner	Abu					2.3- 2.1	
	Con					68- 60	
Mesaphorura macrochaeta Rusek	Abu					9.1- 6.7	
	Con						
Willemia aspinata Stach	Abu						
	Con						
Mesaphorura italica Rusek	Abu						
	Con						
Isotoma hiemalis Schött	Abu						
	Con						
Wankeliella mediochaeta Rusek	Abu						
	Con						
Tullbergia quadrispina (Börner)	Abu						
	Con						
Total of small Tullberginae (Mesaphorura, Karlstejnia, Wankeliella)	Abu	63.4- 6.6	6.3-11.1	12.7- 2.8	9.6-25.2	29.0-24.7	13.6-15.7
	Con	90- 35	75- 80	65- 35	95-100	100-100	100- 94
TOTAL COLLEMBOLA[1]	Abu	108.7-46.9	31.5-44.5	50.1-33.9	40.3-68.7	81.5-87.3	72.7-69.9
Number of species Each sampling		15 20	18 20	18 19	18 18	20 23	18 18
Both samplings		21	21	23	20	24	18

1) **Note:** Species with low abundance (< 1000 m^{-2}) are listed in Table 5.

1,000 m^{-2} in at least one sampling). Abu = abundance given in 1,000 per m^2. Con = constancy, values below 100 m^{-2}. The less common species have been listed in Table 5.

Eu-Pc My		Eu-Pc Dr		Me-Pc ty		Me-Pc At		
A s-a	B s-a	A s-a	B s-a	A s-a	B s-a	A_1 s-a	B s-a	A_2 s-a
11.9- 7.1	9.5-12.1		6.7-17.9	1.5				
1.0- 1.3 42- 55	4.1- 3.9 90- 83	0.2- 0.4 16- 37	10.4-19.5 100- 90		3.2- 4.0 70- 89		0.1- 0.8 5- 21	
	1.0- 0.7	1.7- 6.4	7.7- 7.5	4.0-12.3	5.5- 4.6	0.7- 1.1	0.2	26.4-0.6
5.5 50	16.5-11.5 95-100	3.2- 9.6 74- 95	0.4 10	6.6-20.6 100-100	1.1- 2.1 20- 26	0.6- 1.3 15- 20	2.2- 0.7 42- 21	2.2- 3.2 75- 95
5.8- 6.5 95- 95	2.4- 0.4 75- 22	2.0- 6.8 74- 95	1.2- 2.0 50- 65	1.8 64	0.2- 0.3 20- 16	0.1- 0.1 5- 10	0.4 10	
0.7- 0.4 37- 30	0.5- 0.1 40- 6	0.1- 0.5 11- 32	1.1- 0.5 60- 35	0.1- 1.9 36- 61	0.1 5	0.3- 0.5 20- 25	0.2 10	
3.0- 3.5 79- 95	11.2-13.0 100-100	1.5- 3.8 68- 89	2.9- 6.2 90- 90	0.8-23.9 55-100	2.8- 5.4 85- 89		1.3- 2.0 63- 53	1.4- 1.7 65- 55
3.4- 7.2 84- 90	7.4- 3.2 100- 94	17.8-17.1 100-100	6.5- 4.3 90-100	4.5-77.3 100-100	6.6- 5.4 85- 95	8.2-14.0 100-100	19.0-13.9 100- 89	13.3- 9.5 100- 95
1.4- 1.7 32- 45	4.1- 9.9 90- 89	0.3- 0.1 21- 5	4.3- 7.4 80- 95	+ 9	0.6- 0.4 10- 21	0.3- 0.4 15- 35	0.3- 0.2 16- 16	0.1- 0.2 5- 10
0.3- 0.6 16- 25	3.8- 4.6 80- 78	0.1- 0.3 5- 26	4.4- 8.5 90-100	+ - 0.2 9- 17	0.7- 1.3 40- 58	0.1- 0.7 5- 20	0.3- 0.1 16- 5	0.2- 0.1 10- 5
7.4-32.7 100-100	3.1- 4.3 90- 89	6.0-10.6 100-100	2.1- 3.5 75- 90	4.9-19.2 100-100	2.0- 6.3 80- 84	3.4- 8.3 90-100	1.2- 1.5 58- 42	4.2- 3.1 90- 55
12.2- 2.1 53- 65	0.1- 0.2 5- 22	1.8- 1.4 74- 68	1.0- 0.1 35- 10	3.3- 6.3 82-100	0.8- 0.5 20- 37	3.0- 2.0 90- 80	0.3- 0.2 21- 11	2.0- 0.5 50- 35
9.7-13.3 100-100	18.5-21.2 100-100	18.7-15.7 100-100	57.9-13.9 100-100	16.1-11.9 100-100	17.2-21.1 95-100	45.7-25.9 100-100	24.3-15.2 95- 95	9.8- 3.4 95- 95
8.3- 7.6	2.4- 4.5	3.9- 3.5	10.6- 8.3	4.1- 9.9	6.1-13.9	8.1- 9.0	5.6- 1.5	6.0- 1.0
0.6 30	8.2-14.4 95- 94		7.1- 9.6 90- 90		0.5- 0.4 20- 26	1.4- 2.4 60- 50	0.2- 0.1 11- 11	
	0.1- 2.8 5- 67		0.1 5				0.6-18.9 21- 89	11.6 100
0.9- 2.1	1.6- 0.7		0.1- 0.1	0.2- 1.8	0.1	0.2		0.3
0.1- 0.3 11- 25	0.5- 0.3 30- 22	0.9- 1.0 53- 53	0.1- 0.5 10- 25	1.6 61	0.3 16	1.4- 4.4 65- 90	1.4- 0.5 63- 37	1.3- 3.7 65- 75
0.8- 4.2 47- 90				1.2-12.2 82-100	0.1- 0.4 10- 32	0.7 30	0.1- 0.6 11- 42	0.1 5
	0.1 5			5.5- 0.1 100- 11	0.3- 3.9 15- 58		0.1- 0.5 11- 32	0.1 5
		0.1- 0.4 5- 26						
0.1		0.4- 0.3		1.2- 0.1		2.8- 3.9	0.1	9.9
0.2- 0.3 16- 25	1.3 17	0.2- 0.7 21- 37	0.3- 0.2 20- 20	0.2 27	0.9- 2.6 50- 68	0.1- 1.8 10- 65	0.6- 0.6 32- 42	0.8- 0.2 45- 10
	1.2- 1.1		0.2		10.9- 9.9		0.5- 0.5	
		9.9- 1.1 32- 53		+ - 1.4 9- 61		0.8 50	0.1 11	
		0.1- 0.1	0.1			1.4- 0.3	0.1	
							1.1- 0.4 21- 26	
21.5-16.9 100-100	15.7-19.9 100-100	6.1-10.0 95- 95	25.5-33.8 100-100	10.3-24.2 100-100	28.4-31.7 100-100	13.4-14.2 100-100	6.1- 2.5 47- 37	42.6- 1.5 100- 35
68.1-96.7	96.2-111.5	69.8-80.2	125.2-109.6	64.2-201.4	65.9-86.6	80.9-79.7	60.6-59.7	80.2-41.6
19 19 22 23 22		24 24 24 19 26		25 19 23 21 27		26 23 25 24 29	28	22 24 30

In two habitats (Me-Pc ty and Me-Pc At in area B), a deviating form was found which had a dorsal chaetotaxi like *M. sylvatica*, except that the macrochaetae P_1 on abd. IV were more widely separated than the microchaetae P_2 (as in *M. italica*). This form has also been observed by FJELLBERG (1980). RUSEK (pers. comm.) considered this form to belong to *M. sylvatica*, stressing more the characters on abd. V than on abd. IV. The form is named *M. cf. sylvatica* in the present paper. However, assymetric specimens of this form also occur, with 3 + 2 microchaetae in the a-row on abd. V. These animals have the correct *M. italica* — characters throughout the body on one side (3 microchaetae on abd. V). According to RUSEK (pers. comm.), asymmetric animals should generally be grouped together with the form with the smallest number of setae, as it is not uncommon that extra setae develop. In this case, therefore, the assymetric animals have been pooled with the *M. cf. sylvatica* form.

The existence of two forms showing characters intermediate between *M. sylvatica* and *M. italica* may indicate that these species are only two forms of a larger, variable species. Both species occurred where the two intermediate forms were found. However, I doubt that a combination of these species is fruitful. In most cases, the species are well separated taxonomically. In many habitats, only *M. sylvatica* was found, and *M. italica* was not found at all in area A.

The ultimate answer to these questions probably has to do with the fact that several species (and perhaps all) in the "*Tullbergia krausbaueri*-group" reproduce parthenogenetically (PETERSEN 1971, 1978b). In such case, the species concept is not strictly valid, and mutations may give rise to local forms.

The *Onychiurus armatus* (TULLBERG) *s.l.* — group contains a large number of species which are still not clear systematically. This group has not been further studied in the present case. However, *O. pseudovanderdrifti* Gisin is probably a common species in Norwegian coniferous forest soil.

Folsomia quadrioculata (TULLBERG) and *F. nana* GISIN are also two species or forms where the systematics are not clear. No attempt has been made to distinguish between them here, and the name *F. quadrioculata s.l.* is used.

My specimens of *Hypogastrura scotica* (CARPENTER & EVANS) have a short empodium (shorter than the claw), while the empodium according to GISIN (1960) should be longer than the claw. LEINAAS (1976) found the same deviating character in animals from spruce forest not far from locality B. This form has been listed as *H. cf. scotica* in the present paper.

Concerning the *Isotoma*-species, reference is made to the recent revisions by FJELLBERG (1976b, 1977, 1979). He has also checked the present material. One species, *Isotoma blekeni* LEINAAS, has been described quite recently (LEINAAS 1980).

Two other of the recorded species have been described recently in Norway: *Karlstejnia norvegica* FJELLBERG 1974a and *Folsomia dovrensis* FJELLBERG 1976a.

The identification of the juveniles among *Lepidocyrtus cyaneus* TULLBERG and *L. lignorum* (FABRICIUS) was solved after some problems. The first instar of both species lack scales on the body, but have a pair of scale-like setae dorsally on thorax II. Animals in ecdysis between the first and second instar can be seen to contain scales on the new cuticula. The length of first instar *L. cyaneus* was found to be about 0.48 mm, while first instar *L. lignorum* animals were somewhat larger (about 0.56 mm). From the second stage on, most specimens could be identified by the blue colour in *L. cyaneus*. A valuable help for the solution of this problem was information given by LEINAAS, that *L. lignorum* hatch in spring, while *L. cyaneus* hatch in the summer. A second hatching of *L. lignorum* may occur in the autumn, resulting in a mixture of juvenile forms of the two species.

In *Willemia anophthalma*, some animals with deviating and also asymmetric chaetotaxi on abd. IV were observed. Some had only two pairs of hairs along the dorsal midline which is characteristic for *W. scandinavica* STACH. However, other characters showed that these animals belonged to *W. anophthalma*.

Among Sminthuridae, only a part of the material could be identified, as juvenile stages dominated.

4. Results

4.1. The total Collembola fauna of the habitats

Table 4 contains information on the abundance and constancy (frequency) of the most abundant Collembola species in the various sampling plots. The soil fertility increases from left to right in the table. Species occurring in the poorest soils are listed first. On the top of the table, the vegetation types are indicated, together with the study area and season.

The small Tullberginae (mainly *Mesaphorura*-species, which correspond to „*Tullbergia krausbaueri*") made up a substantial part of the Collembola fauna in all habitats, and their total abundance etc. is therefore summed up near the bottom of the table. Because of the use of sub-samples, data on constancy were not achieved for these species.

The total abundance of Collembola varied from 31,500 m^{-2} (Cl-Pn, area B, spring), to 201,400 m^{-2} (Me-Pc ty, area A, autumn). The next highest value, 125,200, was, however, well

below the maximum. Thirteen of the fifteen observations were rather evenly dispersed between the approximate limits 30,000—110,000 m^{-2}.

There was no systematic change in abundance from spring to autumn. In eight localities, autumn values were higher than spring values, while the opposite occurred in seven sites.

Table 5 shows the occurrence of the less abundant species (with abundance below 1,000 m^{-2}). Detailed information on abundance and constancy of these species, as well as data on dominance and variation between soil cores for all species have been omitted in this paper, but interested readers can achieve the data from the author.

If we disregard the relatively few animals which could not be identified to species level, and also *Mesaphorura cf. sylvatica*, which perhaps should be pooled with the "normal" *M. sylvatica*, the list contains 60 species. The total number of species recorded in the various habitats is listed at the bottom of Table 4, and also the species numbers at each seasonal sampling. The categories not identified to species level were included if it was clear that they represented additional species. The lowest number in any sampling was 15 (Cl-Pn in area A, spring sample) and the highest 26 (Me-Pc At in area A [site A_1], spring sample). In most habitats, the species numbers recorded in spring and autumn were not very different, and the discrepancy was mainly due to the occasional presence of rare species. The total species numbers found in a sampling site varied from 18 (Va-Pn, area B) to 30 (Me-Pc At, site A_2, which had the richest soil of all).

4.2. Species-area curves

The species numbers recorded are comparable due to corresponding numbers of samples taken in the various habitats. However, as each plant community evidently contains a relatively high proportion of rare Collembola species (Fig. 6), further sampling would certainly have revealed more species in all sites. In the present study, the main purpose was to record a large enough proportion of the species to allow some general conclusions about the Collembola fauna. Whether this intention was realized, can be decided from "species-are curves" (Fig. 5), where the cumulative number of species is plotted against sample numbers (expressing sampling area). The majority of species in a given sampling were usually achieved after about ten soil cores, and the curves often started to level off after about five samples. The spring samples in area A were an exception, showing a steady increase in species numbers up to about fifteen samples or even more in several sites. In the last five samples, the number of new species was very low in most cases. When we disregard the samplings with less than twenty samples (due to accidental loss of samples), the mean increase in species numbers from fifteen to twenty samples was 1.2. This indicates that the chance of finding additional species was now low, and that twenty samples was sufficient for a broad characterization of the fauna at each season.

Both spring and autumn samples were taken, in order to catch species with different life cycle patterns. However, the number of new species found in the autumn sampling was low (mean value 3.1). In most sites the species numbers recorded at the two samplings were rather similar.

4.3. Dominance structure and diversity

The dominance data for the whole material have been illustrated by histograms in Fig. 6. In all samplings, the dominance distribution was very skew, with high numbers of species with low dominance and a small number of species with high dominance. A large fraction of the species had a dominance of less than 1 %. This category represented from 28 to 62 % of the species, most values lying between 40 and 55 %. The fraction of "rare species" was lowest in Eu-Pc My (32—39 %), and highest in the richest soil (Me-Pc At, 46—62 %).

With approximately 20—25 species, the average dominance value would be 4—5 % for each species. In the present samplings, only 3—9 species showed dominance values above 5 %. The very few species achieving dominance values above 20 % are named in Fig. 6.

Table 5. Occurrence of less common species (< 1,000 m^{-2}) in the various habitats. This list is a supplement to Table 4, which contains the more common species

Species	Vegetation type														
	Cl-Pn		Ba-Pn		Va-Pn		Eu-Pc My		Eu-Pc Dr		Me-Pc ty		Me-Pc At		
	Study area														
	A	B	A	B	A	B	A	B	A	B	A	B	A_1	B	A_2
Bourletiella pistillum GISIN	+														
Entomobrya nivalis (L.)	+				+						+				
Orchesella bifasciata NICOLET	+	+	+		+					+	+				
Sminthurinus aureus (LUBBOCK)	+		+						+		+		+	+	+
Sminthuridae spp. juv.	+		+		+		+	+	+	+	+	+	+	+	+
Pseudachorutes dubius KRAUSBAUER			+												
Hypogastrura denticulata (BAGNALL)			+												
Entomobryidae, juv.	+		+		+			+	+		+				
Hypogastrura cf. scotica (CARPENTER & EVANS)			+						+				+		+
Folsomia spp., juv.			+		+				+						+
Tomocerus flavescens (TULLBERG)			+					+					+	+	+
Neanura muscorum (TEMPLETON)			+	+	+	+	+	+	+	+	+			+	+
Pseudachorutes parvulus BÖRNER				+	+										
Folsomia dovrensis FJELLBERG					+				+		+	+	+		
Sminthurinus flammeolus GISIN							+								
Sminthurides pumilis (KRAUSBAUER)							+				+		+		
Anurida granulata AGRELL								+		+			+		
Sminthurus lubbocki TULLBERG									+						
Dicyrtoma fusca (LUCAS)									+				+		
Willowsia nigromaculata (LUBBOCK)										+					
Dicyrtoma cf. minuta juv. (FABRICIUS)											+				
Isotoma blekeni LEINAAS												+			
Hypogastrura socialis (UZEL)												+			
Mesaphorura cf. *sylvatica* RUSEK												5[1])		+	
Proisotoma minima (ABSOLON)													+		
Sminthurides parvulus (KRAUSBAUER)													+		
Arrhopalites cochlearifer GISIN													+		
Arrhopalites spp., juv.													+	+	+
Isotoma neglecta SCHÄFFER														+	
Sminthurus fuscus (L.)														+	
Onychiurus serratotuberculatus STACH															+
Folsomia cf. *candida* juv. (WILLEM)															+
Anurida granaria (NICOLET)															+
Arrhopalites caesus (TULLBERG)															+

[1]) Mean abundance of 5,000 m^{-2} in one site, but excluded from Table 4 due to unclear taxonomic status.

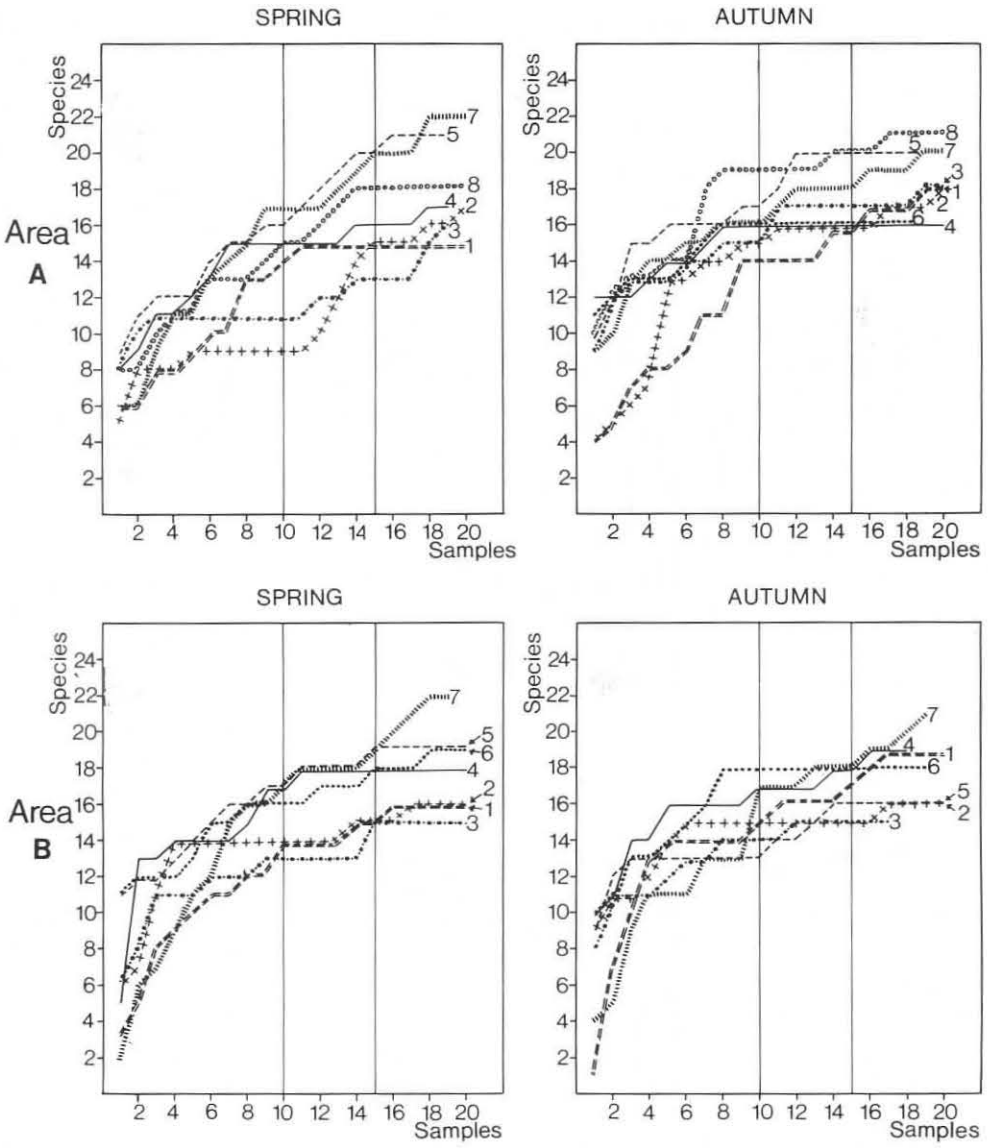
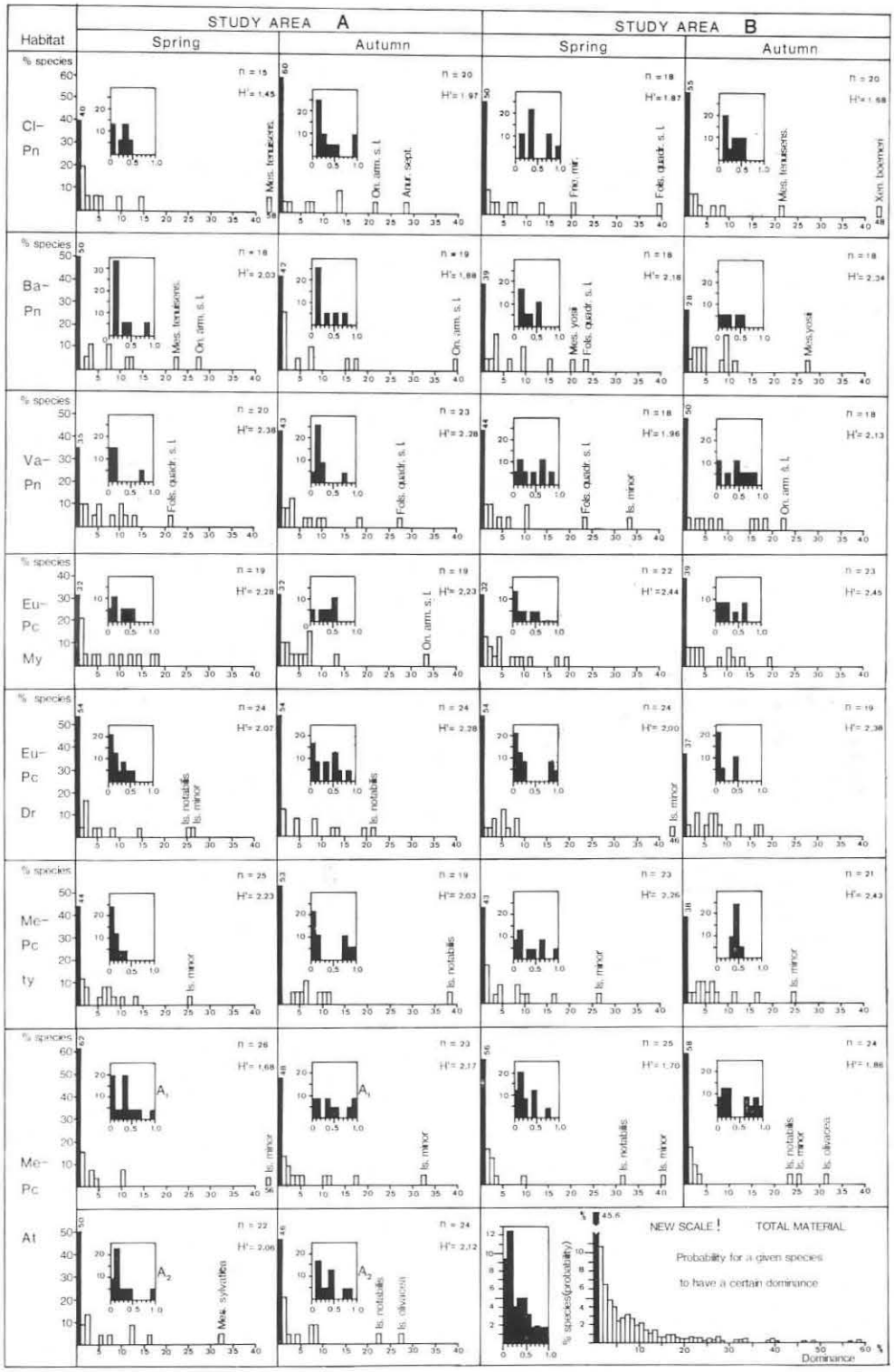


Fig. 5. Species-area curves for all samplings. Cumulative number of species is related to sample numbers. In the spring sampling of area A, locality 6 has been excluded due to deviating sample size. Symbols for vegetation types are given in the lower part of the figure.


Habitat
STUDY AREA A
STUDY AREA B
Spring
Autumn
Spring
Autumn
% species
Cl-Pn
Ba-Pn
Va-Pn
Eu-Pc My
Eu-Pc Dr
Me-Pc ty
Me-Pc
At
NEW SCALE !
TOTAL MATERIAL
Probability for a given species to have a certain dominance
% species (probability)
Dominance

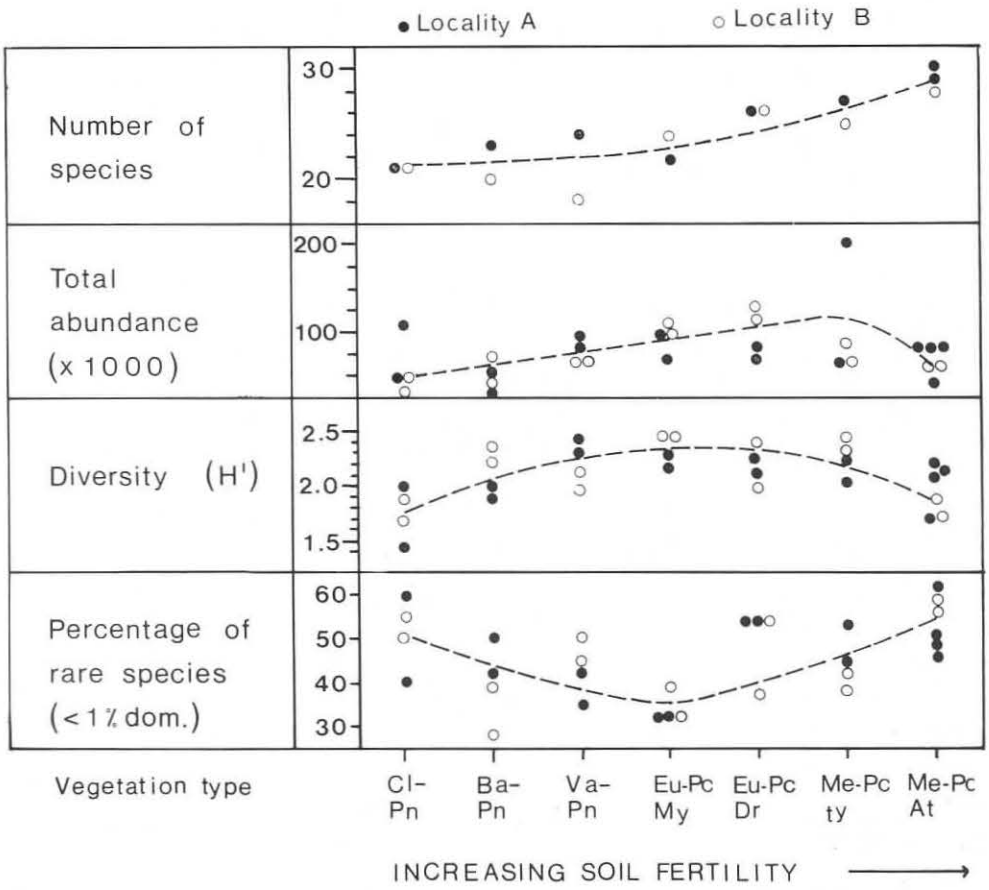
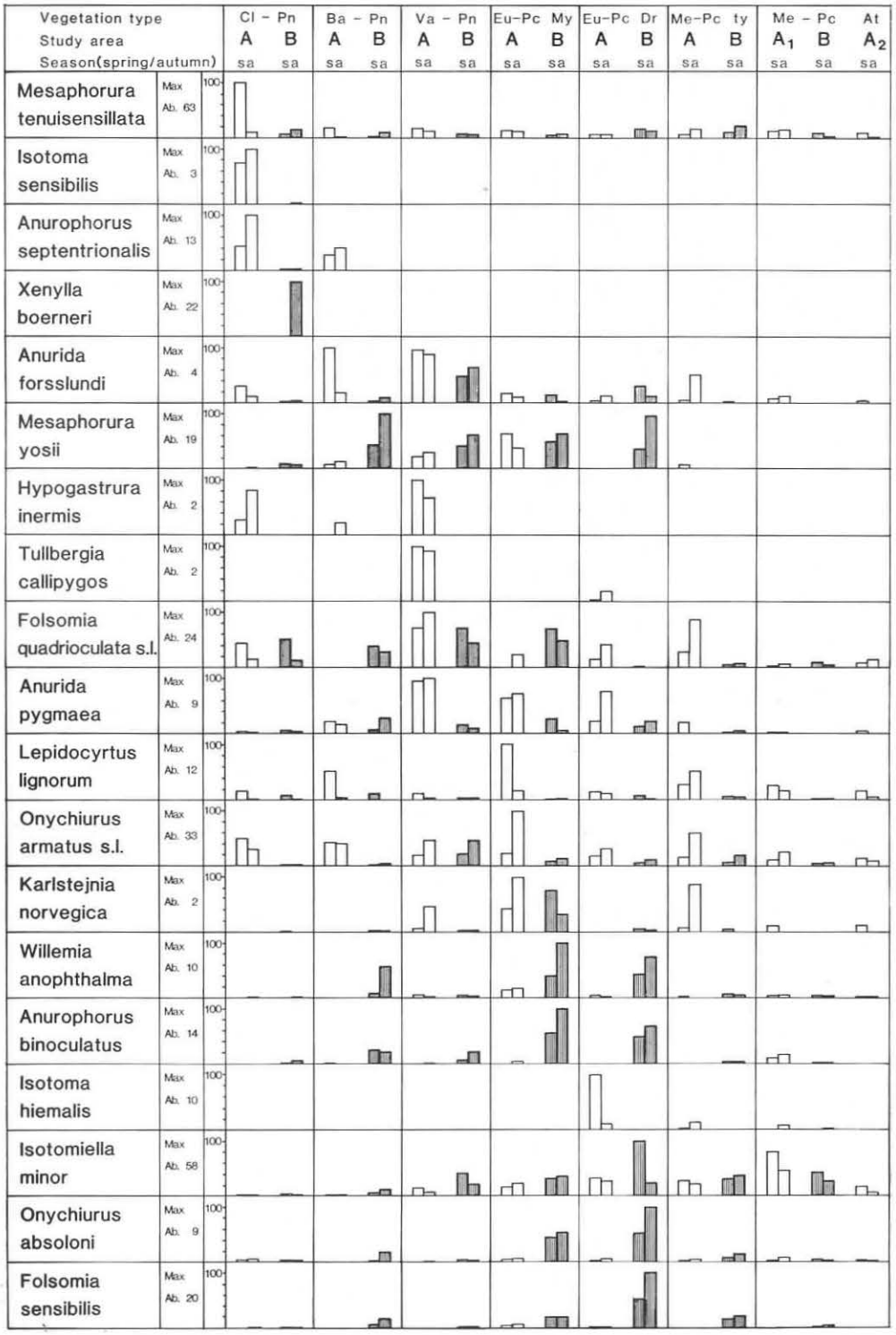


Fig. 7. Relationships between vegetation type and soil fertility on one hand, and four central parameters for the Collembola communities on the other hand.

Fig. 6. Distribution of the dominance values for the various species at each sampling. The horizontal axis gives the dominance value, while the vertical axis indicates the per cent of the species which fall into the various dominance classes (range: 1 %). Because of the high percentage of species with dominance values below 1 %, the distribution within this range has been further split up in ranges of 0.1 %. For each sampling, the following information is also given: total number of species (n), the SHANNON-WIENER diversity index (H'), and the names of species with dominance values above 20 %. Bottom right: Mean distribution of dominance values based on all samplings. This indicates the probability for a given species to have a certain dominance value.


Vegetation type
Study area
Season(spring/autumn)
Cl - Pn
Ba - Pn
Va - Pn
Eu-Pc My
Eu-Pc Dr
Me-Pc ty
Me - Pc
At
A
B
A1
A2
sa
Mesaphorura tenuisensillata
Isotoma sensibilis
Anurophorus septentrionalis
Xenylla boerneri
Anurida forsslundi
Mesaphorura yosii
Hypogastrura inermis
Tullbergia callipygos
Folsomia quadrioculata s.l.
Anurida pygmaea
Lepidocyrtus lignorum
Onychiurus armatus s.l.
Karlstejnia norvegica
Willemia anophthalma
Anurophorus binoculatus
Isotoma hiemalis
Isotomiella minor
Onychiurus absoloni
Folsomia sensibilis
Max
Ab. 63
Ab. 3
Ab. 13
Ab. 22
Ab. 4
Ab. 19
Ab. 2
Ab. 2
Ab. 24
Ab. 9
Ab. 12
Ab. 33
Ab. 2
Ab. 10
Ab. 14
Ab. 10
Ab. 58
Ab. 9
Ab. 20
100

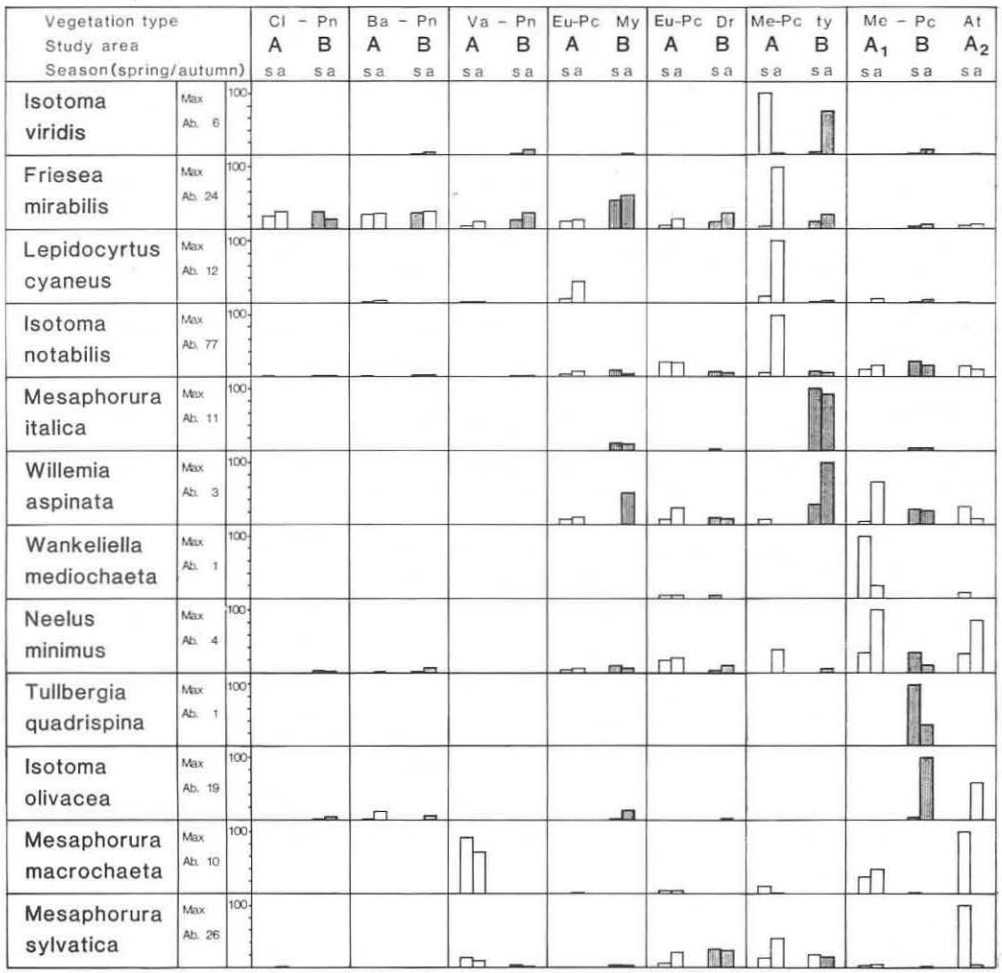


Fig. 8 (A & B). Relative abundance on the various plant communities for the 31 Collembola species which at least in one site achieved an abundance of 1,000 m^{-2}. The highest abundance noted for each species has been set to 100 %. The maximum values are given after each species name (in thousands per m^2). Study area A: open columns, study area B: shaded columns. Soil fertility increases from left to right.

In Fig. 6, the distribution of rare species has been analyzed further by dividing the range of 0—1 % dominance into ten parts. There is a general trend for increasing number of species with reduced dominance values also within this very lowest section of the scale. In the lower right of the figure, the mean distribution of dominance values from all samplings has been drawn, including a separate histogram for the 0—1 % area. The curves should be considered as the distribution of probability for a given species to have a certain dominance value. In the curve based on 1 % intervals, there is a steep increase with lowered dominance values, and almost every second species (46 %) has a dominance of less than 1 %. A further analysis of this category based on 0.1 % intervals gave a similar curve, revealing that on the mean, more than 20 % of the Collembola species had dominance values below 0.2 %.

Diversity is often expressed by the SHANNON-WIENER index (SHANNON & WIENER 1963). Given a certain number of species, the index reaches its maximum value if all species are equally abundant. It is written $H' = -\sum_{i=1}^{S} p_i \ln p_i$,

where S is the number of species and p_i is the fraction of each species.

The values for each sampling are given in Figure 6. The Eu-Pc My samplings gave rather high values (up to 2.45), due to relatively few numbers of both very rare and very dominating species. Another high value (2.43) was found in Me-Pc ty, autumn, area B, where a large proportion of the species were centered around the arithmetic mean value of 5 % dominance. Values below 2 were obtained only where one, two or three very dominant species occurred. The lowest value, 1.45, was found in Cl-Pn, spring, area A, where one species made up 58 % of all Collembola.

4.4. Soil fertility related to species numbers, abundance, diversity and proportion of rare species

To give an overview of some main trends in the Collembola material, the relations between the above-mentioned factors and the vegetation types have been put together in Fig. 7. The stippled lines are approximate and meant only to show trends in relation to soil fertility. While the number of Collembola species seems to increase with increasing soil fertility, the total abundance tends to be highest at the Eu-Pc Dr/Me-Pc ty level. Diversity and percentage of rare species show inverse patterns, with maximum and minimum values respectively in the middle part of the gradient.

4.5. Relations between Collembola species and plant communities

4.5.1. Distribution of single species

The quantitative distribution of the 31 most abundant species (with an abundance of 1,000 m^{-2} in at least one site), appears by a close examination of Table 4. A large-scale comparison was made between these species based on the vegetation types supporting the highest populations. The comparison was complicated by the facts that several species were more common in one study area than in the other, and that the highest abundance values were often noted in different plant communities in the two areas (Fig. 8). However, for each species, a certain part of the soil fertility gradient covered the highest abundance values. This allows us to construct a simplified diagram which indicates the main range of occurrence for each species (Fig. 9). Although the length of the sections to a certain degree is subjective, it is meaningful to relate the occurrence of the vairous species to the fertility gradient. For most species, a continuous section of preference could be indicated. Furthermore, the preferred sections for the various species were well distributed along the whole gradient. The sections varied greatly in length, from being restricted to one special plant community to covering the whole gradient.

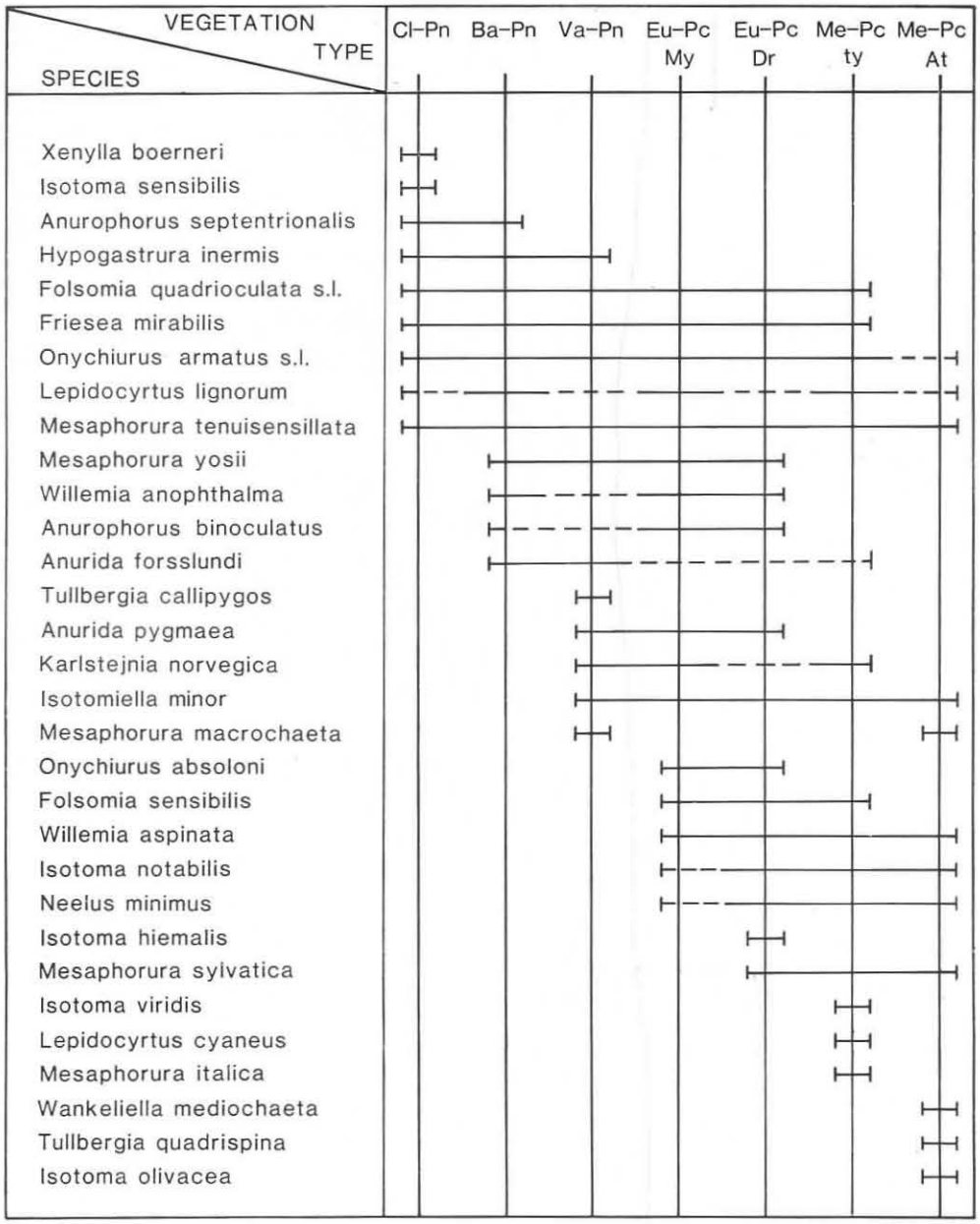


Fig. 9. The main range of occurrence for each of the most abundant Collembola species, related to vegetation types and soil fertility. Data from all samplings in both study areas have been used. Stippled line indicates doubtful inclusion into the "main range", due to lower numbers.

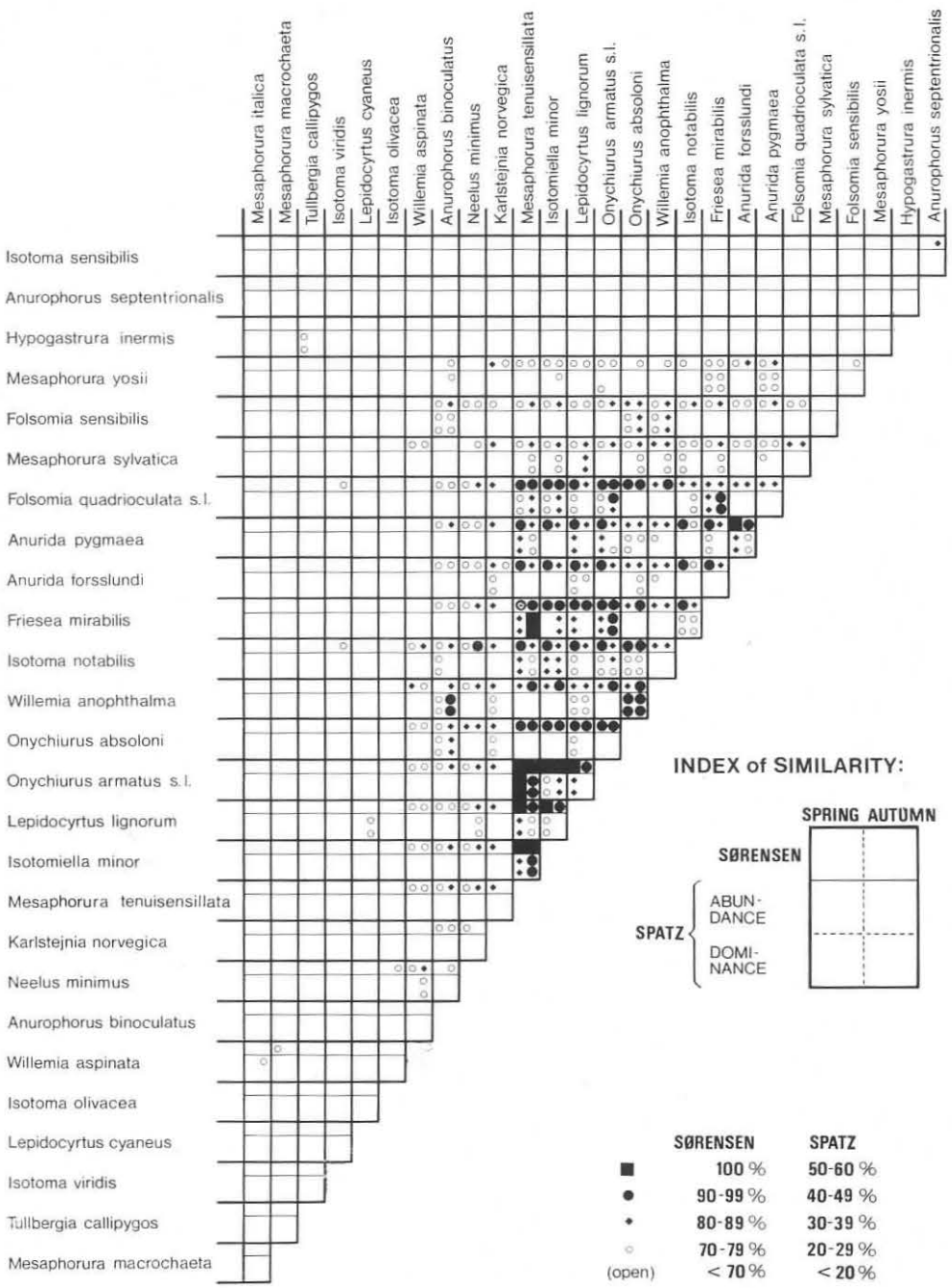


Fig. 10. Indexes of similarity between species pairs of Collembola. For each pair, six index values have been calculated, and are located in the matrix as shown in the inset figure. The indexes are based on data from all samplings in both study areas. Further information is given in the text.

4.5.2. Similarity indexes for pairs of species

Some species showed large differences in their distribution on the various plant communities, while other species had similar distribution patterns. The degree of similarity in the distribution on all the fifteen sampling plots has been calculated for all pairs of the 31 species shown in Fig. 8—9. There are three possible bases for such a comparison: (1) simply presence or absence in the various plots, (2) abundance data, and (3) dominance data. Indexes have been calculated in all three ways both for spring and autumn data, which gives six indexes for each pair of species. SØRENSEN's index was used for the first category and SPATZ' index for the two other categories. The principles for both indexes have been explained earlier. However, in the present case, the data have been treated with respect to species, and not with respect to habitats, as in chapter 2.4.2.

Fig. 10 shows the results of these calculations. Four species had so low index values with regard to all other species that they were excluded from the figure: *Xenylla boerneri*, *Isotoma hiemalis*, *Wankeliella mediochaeta* and *Tullbergia quadrispina*. The various levels of similarity have been indicated by symbols in the figure. It is a problem to compare the values from the two types of indexes, since for instance 50 % similarity is a low value for SØRENSEN's index, while it is one of the highest values obtained by SPATZ' index. An attempt has been made to adjust the grouping of values so that the same symbols could be used for both indexes (bottom of Fig. 10).

There is a rather large number of species pairs with high values of SØRENSEN's index ($\geqslant 90$). In all cases, the reason for the high correlation is that they occur either in all or in most of the relevant habitats. High values were never obtained between species which occurred in only a restricted number of sites.

The index of SPATZ is a good expression of the ecological similarity between species, since also quantitative data are taken into consideration. There was a comparatively large variation in these index values, and only a limited number of species pairs achieved values in the upper range of the scale ($\geqq 40$ % similarity). However, using this index all the high values obtained between common species were also distributed over all or most of the gradient. An interesting point is that some "common" species had such a deviating distribution on the habitats, both regarding abundance and dominance, that their similarity with other species never reached any of the two highest levels. These species were *Anurida pygmaea*, *Anurida forsslundi*, *Isotoma notabilis* and *Lepidocyrtus lignorum*. The highest similarity indexes on a quantitative base were achieved between *Mesaphorura tenuisensillata* and two other species: *Friesea mirabilis* and *Onychiurus armatus s.l.*, respectively. Their common feature was a rather even abundance on most habitats, with values around an approximate mean level of 5,000—10,000 m^{-2}. The species pair with the next highest similarity to these was *Willemia anophthalma* — *Onychiurus absoloni*. They were both abundant in Eu-Pc My and Eu-Pc Dr in study area B, with low abundance in most other sites.

4.6. Relations between plant and Collembola communities

Collembola communities were related to the different vegetation types in the same way as explained in chapter 2.4.2. The results based on SØRENSEN's index (i.e. species composition) appear in Fig. 11. The similarity indexes between the fauna in corresponding plant communities are enclosed in bold frames. Only once did these values exceed 80 % (between the two Eu-Pc My localities in autumn). Most of them were rather low in autumn (< 60 %). However, in spring, similarity indexes between the fauna in corresponding vegetation types were between 70 and 80 % in most cases.

The highest similarity indexes for species composition of Collembola (> 80 %) were often between different vegetation types in area B. Similarity indexes between habitats in area A never did reach such high values.

The lowest values were mainly found among the "poorest" and "richest" soils. One exception was Ba-Pn in area A, which in the autumn had a species composition which was very different from most other sites.

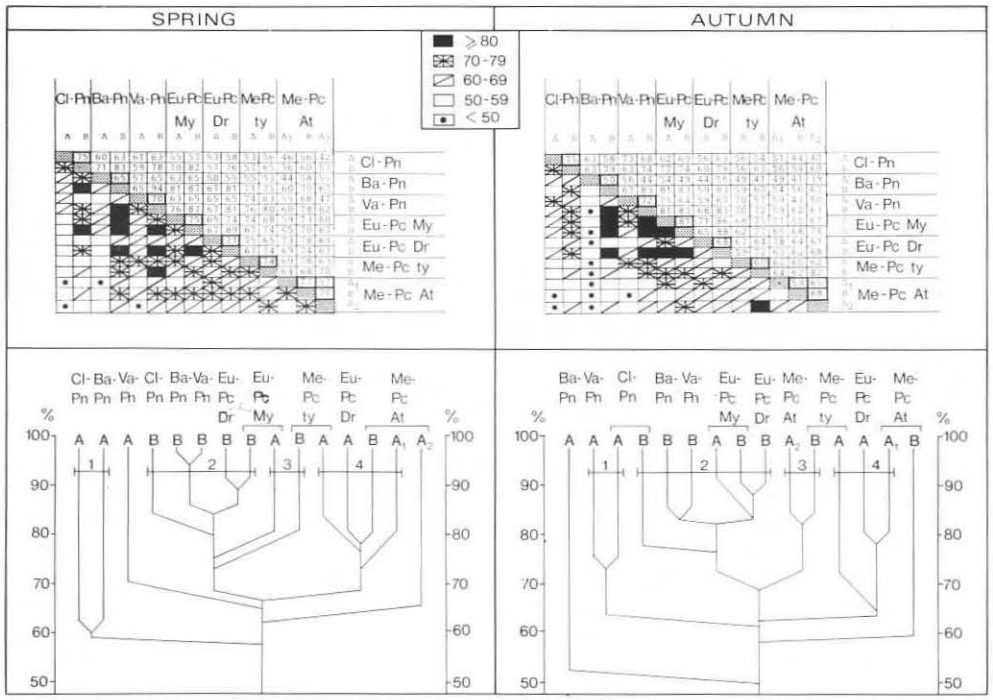


Fig. 11. Similarity between Collembola communities in different vegetation types, based on the index of SØRENSEN. In the lower half, the communities have been classified into natural groups. Corresponding information on floristic similarity is given in Figure 1.

Based on species composition, most Collembola communities fall within one of four groups (lower part of Fig. 11). The strong influence of sampling area is well illustrated for both seasons, since habitats from the same area tend to be grouped together. However, the system is also related to soil fertility, since the habitats in each group represent a certain section of the soil fertility gradient.

Neither when the Collembola communities were compared on a quantitative base (by applying SPATZ' index on abundance and dominance data) were the highest indexes between corresponding vegetation types (Fig. 12, bold frames). Again, most of the highest index values were between different habitats in area B. In fact, the Collembola communities in corresponding vegetation types were often rather dissimilar and only in three cases did index values exceed 25 %.

Quite parallel to Fig. 11, SPATZ' index gave lowest similarity values between the "poorest" and "richest" soils (Fig. 12). The grouping of Collembola communities was very similar on the basis of abundance and dominance data. The two first groups had much in common with those achieved from SØRENSEN's index, but groups 3 and 4 were different. Group 3 consisted only, or mostly, of habitats from area A. In Fig. 12 as well, however, the groups represented different levels of soil fertility.

We have until now focused upon the combinations with the highest or lowest index values, and the natural groupings of the Collembola communities. Another viewpoint is to ask for each community: which other site has the most similar Collembola fauna? If the community in question is rather specific, all similarity indexes with other sites may be rather low; but in any case the point is to pick out the highest of them. Such relations are illustrated in Fig. 13. From each Collembola community, an arrow goes to the one which showed the greatest similarity, either based on species composition (SØRENSEN's index) or on quantitative data (SPATZ' index). In some cases, two or even three other communities gave the same index values.

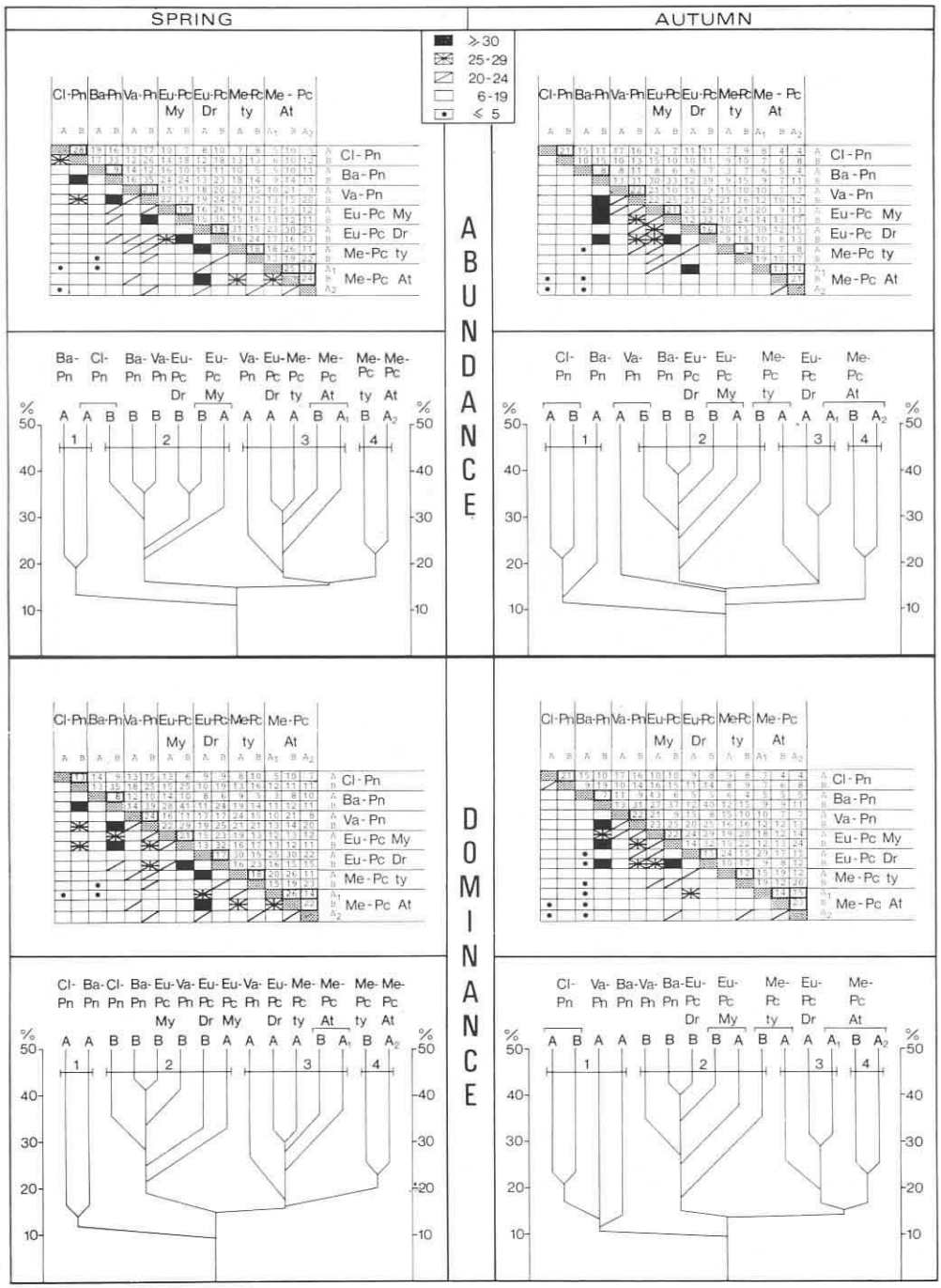


Fig. 12. Similarity between Collembola communities in different vegetation types, based on the index of Spatz (using abundance and dominance data). The communities have also been classified into natural groups. Corresponding information on floristic similarity is given in Figure 1.

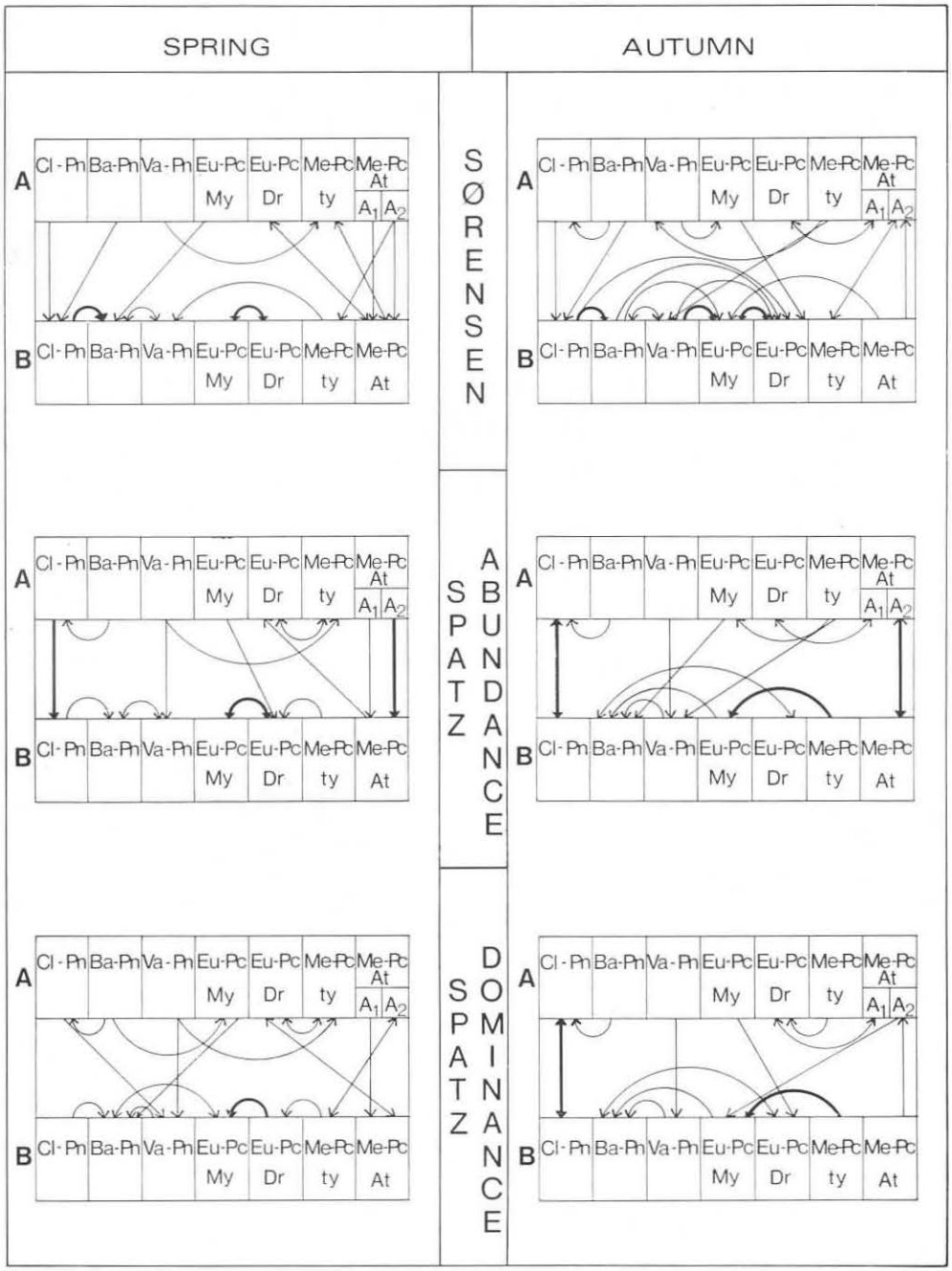


Fig. 13. Simplified presentation of the similarity between Collembola communities in all sampling plots. Vegetation types and study area (A or B) are indicated. From each site, an arrow goes to the one which showed the largest similarity in the structure of the Collembola community. Soil fertility increases from left to right. Bold arrows indicate connections common for plant and Collembola communities.

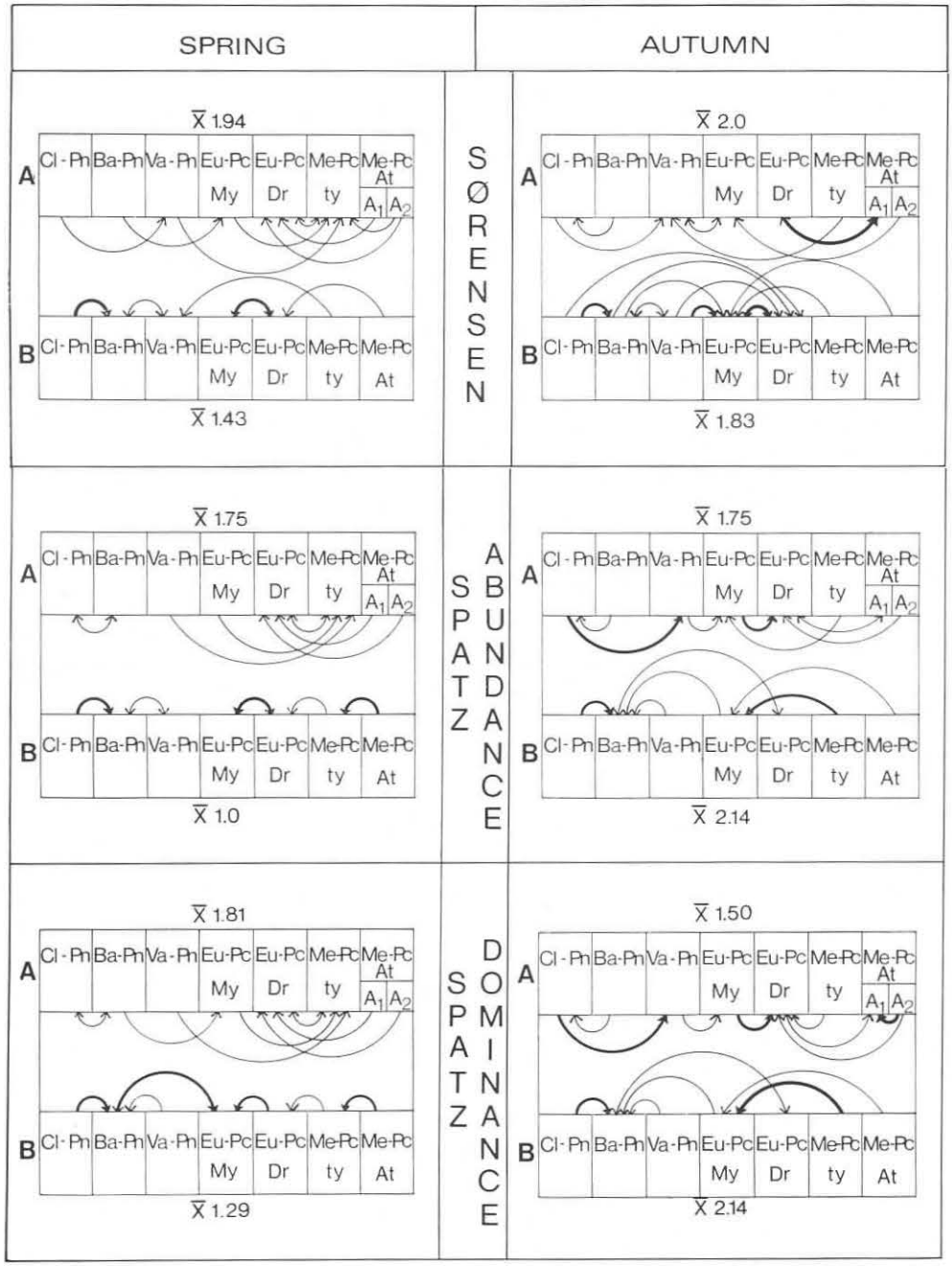


Fig. 14. Connetions between Collembola communities illustrated as explained in Figure 13, but only considering internal connections within each study area. Bold arrows indicate connections common for plant and Collembola communities. The mean number of steps covered by an arrow has been calculated.

Fig. 13 confirms the high number of internal linkages in area B, and also illustrates several connections between different vegetation types in different study areas. However, at each end of the soil fertility scale, arrows often combined Collembola communities in corresponding vegetation types. This appears from both types of indexes. A corresponding linkage exists on the Va-Pn level based on quantitative data (SPATZ' index).

The relationships between Collembola and plant communities have to this point been based on the system of vegetation types. However, as shown in Fig. 1, when all plant species, and not only the "indicator" species, are taken into consideration, the connections between the various plant communities in many cases deviate from the system of vegetation types. If a figure corresponding to Fig. 13 is drawn for plant communities, a comparison of arrows in the two figures is a very direct way of comparing faunal connections with floristic connections. The bold arrows in Fig. 13 represent the connections which are common for Collembola and plant communities. However, only a few of the non-vertical arrows are "explained" in this way.

One reason for the apparently few relations between Collembola and plant communities is that the two study areas are different, both regarding Collembola and vegetation. Therefore, a more fruitful approach may be to compare only sites within the same study area. Such relations have been drawn in Fig. 14. Short arrows indicate that neighbouring vegetation types on the soil fertility scale also have Collembola communities with greatest similarity.

In one case, this type of relationship between Collembola and plant communities was as good as possible, since all arrows pointed to a neighbouring habitat (Fig. 14, by applying SPATZ' index to the abundance data from spring in area B).

A quantification of this correlation was made by calculating the mean number of steps covered by all arrows. If two or more arrows left the same site, the mean length of these was first calculated. A_1 and A_2 were treated as separate vegetation types in this connection. All the mean values, which have been noted in Fig. 14, were lower than if the length of the arrows had been random (3.0 steps in area A and 2.67 steps in area B).

Bold arrows in Fig. 14 indicate that corresponding floristic connections exist. It is interesting to note that some of the long arrows are common to Collembola and vegetation.

5. Discussion

5.1. Species numbers, abundance, diversity and proportion of rare species

The relations observed between soil fertility and the above-mentioned factors (Fig. 7) are not easy to explain. However, it is interesting to note that the number of Collembola species follows the same trend as the number of plant species, with rather low values in the four "poorest" soils, and an increase within the three "richest" soils (Table 2). It may be that a more varied litter, consisting of remnants from a large number of plant species, contributes to a greater number of niches for the Collembola. Changes in soil texture, chemistry and microflora may also be of importance.

The abundance of Collembola also tended to increase with increased soil fertility, but only up to the Eu-Pc Dr/Me-Pc ty level. In the richest plant community, the numbers were again relatively low. In the poorest sites, dry conditions (except in Ba-Pn), low pH and low decomposition rates may be limiting factors. The medium rich sites have sufficient moisture, probably better food conditions due to a more active fungal flora, and limited competition from larger invertebrates. In the richest habitat, larger invertebrates, like Lumbricidae, Myriopoda, Isopoda, Coleoptera and Mollusca, are abundant and may in various ways depress the Collembola numbers. It is also well known that fungi, a main food item for Collembola, may be scarcer in rich soils.

Apparently, the highest diversity occurred in the medium part of the gradient. To a large degree, the diversity is influenced by the percentage of rare species ($< 1\%$ dominance), since these two curves have opposite shapes. However, both the species numbers and the distribution of the "common" species are also important. The Eu-Pc My habitats, with the highest

diversity indexes, had both few rare and few very abundant species, and several species had dominance values not far from the "ideal" value of 5 %. In a count of these samples, five to ten random animals might all represent different species. The observed trend can indicate that in the middle of the gradient, a comparatively large proportion of the niches have a large spatial distribution.

The following comparison of abundance data is restricted to studies where extraction was performed in a "high gradient" apparature. In Swedish pine forests, most abundance data for Collembola lie between 40,000 and 90,000 m^{-2} (Axelsson *et al.* 1973, Persson 1975, Wirén 1975, Lohm *et al.* 1977, Bååth *et al.* 1980). This range corresponds well with the present study. The few samples from spruce forest (Eu-Pc My) taken in Sweden and Finland are surprisingly low, all values being below 50,000 m^{-2} (Huhta & Koskenniemi 1975, Huhta 1976, Bengtsson & Rundgren 1980). However, Leinaas' (1976) samplings in a Norwegian Eu-Pc My habitat throughout the year gave values between 70,000 ad 140,000 m^{-2}, most values being near 100,000. This level is in good accordance with the present results.

The fact that species numbers depends on the number and size of the samples (i.e. sampling area), makes a direct comparison with species numbers in other studies impossible. However, in most Swedish reports from coniferous forest (see above, and chapters 1 and 5.2.2.), between 15 and 25 species were recorded. These values resemble the numbers from individual samplings in the present study. The highest number of species from Scandinavian coniferous forest sites, 44, was noted by Leinaas (1976) in his intensive sampling over one year in a Eu-Pc My locality. His total number of soil cores was 480, each covering 10 cm^2. However, within one sampling series of 20 soil cores, the number of species never exceeded 25. Probably his locality was not exceptionally rich in species. To his species list should also be added some *Mesaphorura* species, which were collectively named *Tullbergia krausbaueri*. Further intensive studies may very well reveal that species numbers around 50 or above are common in coniferous forest soils.

The high proportion of rare species noted in the present study is confirmed by compiling data from recent Scandinavian studies in coniferous forest soil, encompassing 28 different samplings (Axelsson *et al.* 1973, Bödvarsson 1973, Persson 1975, Wirén 1975, Leinaas 1976, Lohm *et al.* 1977, Bååth *et al.* 1980 and Bengtsson & Rundgren 1980). Although the proportion of rare species certainly depends on the sample size, it is interesting to note that on the mean, 49.4 % of the species had dominance values below 1 %. This value is close to the mean value in the present study (45.6 %).

The large fraction of rare species raises two questions: What is their function, and how can they survive in so small numbers? On the community or ecosystem level their function may be to take over in special microhabitats in the forest, or to take over in the ordinary soil community during long-term changes (as climatic changes etc.). Obviously the rare species may in certain situations represent a valuable genetic reserve. However, if the species depend on sexual reproduction, it is difficult to understand how individuals of different sexes may meet. Very often, only one specimen in one soil core is found. Either the extraction efficiency is low for several such species, or a higher number of species than we know of may reproduce parthenogenetically. The rare species may also prove to be very aggregated, surviving only in certain microsites.

5.2. Relations between Collembola species and plant communities

5.2.1. General trends

Fig. 9 indicated that the distribution of most species can be related indirectly to plant communities through soil fertility. However, as several other factors also change with increasing soil fertility (e.g. soil pH, N-content, loss on ignition, humus type), the ultimate regulating factor(s) may vary from species to species.

It is interesting to note that the five closely-related *Mesaphorura*-species, formerly treated as one species *(Tullbergia krausbaueri s.l.)*, showed different distribution patterns on the various plant communities (Fig. 9). This indicates that the splitting is ecologically valid.

The abundance maxima for the different species were fairly evenly distributed on the seven vegetation types. Four species reached their highest abundance in Cl-Pn, two in Ba-Pn, four in Va-Pn, five in Eu-Pc My, four in Eu-Pc Dr, six in Me-Pc ty and six an Me-Pc At (cf. Fig. 8). Apparently, each level of the soil fertility gradient favours certain species.

5.2.2. Comparisons with other studies in Scandinavian coniferous forest

Limited information is available from Scandinavia on the distribution of the species in various vegetation types of coniferous forest. In Norway, LEINAAS (1976) studied the Collembola fauna in a Eu-Pc My habitat. In Sweden, most investigations have been made in poor sites with Scots pine forest (AGRELL 1941, AXELSSON *et al.* 1973, BÖDVARSSON 1973, PERSSON 1975, WIRÉN 1975, LOHM *et al.* 1977, BÅÅTH *et al.* 1980). BÖDVARSSON (1973) also investigated two sites with a vegetation close to Eu-Pc Dr, and BENGTSSON & RUNDGREN (1980) studied several sites with Eu-Pc My vegetation. FORSSLUND (1944) investigated habitats with three different plant communities corresponding approximately to Eu-Pc My, Eu-Pc Dr and Me-Pc At. Comparisons between these various studies are difficult due to different extraction techniques (Berlese funnels were used by AGRELL, FORSSLUND and BÖDVARSSON), different sampling times, and in some cases a low number of samples. However a few considerations can be made for some species.

A wide range of occurrence can be confirmed for *Friesea mirabilis*, *Onychiurus armatus s.l.*, *Lepidocyrtus lignorum* and *Isotomiella minor*. These species are probably among the most typical for Scandinavian coniferous forest habitats. *Folsomia quadrioculata s.l.* was absent in the areas studied by FORSSLUND (1944) and LEINAAS (1976), but it has been found in both poor pine forest sites and in rather rich spruce forest (Eu-Pc Dr, BÖDVARSSON 1973).

A preference for poor pine forest sites is obvious for *Anurophorus septentrionalis*. This species was earlier confused with *A. laricis* NICOLET, until PALISSA (1966) revealed their difference. *A. laricis* is characteristic for very dry and exposed habitats, such as tree trunks, stones, etc. (FJELLBERG 1980), and older records of "*A. laricis*" from forest litter probably refer to *A. septentrionalis*. In the several pine forest sites investigated in Sweden, this species occurred regularly and was sometimes among the most abundant species. In dry pine litter without vegetation, a dominance of 85 % was recorded by AGRELL (1941). BÖDVARSSON (1973) found a dominance value of 51 % in a Ba-Pn/Va-Pn habitat, and BÅÅTH *et al.* (1980) noted 17 % dominance in a Va-Pn habitat. The species may also occur in Eu-Pc My communities (FORSSLUND 1944, LEINAAS 1976, HÅGVAR unpubl.), and in low numbers even in Eu-Pc Dr (FORSSLUND 1944), but in spruce forest this species is probably limited to drier microsites.

Willemia anophthalma and *Anurida pygmaea* are evidently common inhabitants of Scandinavian Eu-Pc My and Eu-Pc Dr habitats, but may also be numerous in pine forest soil. High numbers of these species noted by FORSSLUND (1944) in two samples from a Me-Pc At site is in conflict with the present results. For *W. anophthalma*, this may be due to a confusion with *W. aspinata*.

Eu-Pc My and Eu-Pc Dr seem to be the favoured habitats also for *Anurophorus binoculatus* and *Onychiurus absoloni*. FORSSLUND (1944) found the two species abundant in these vegetation types, while Me-Pc At gave fewer animals. In the Swedish pine forests referred to earlier, *A. binoculatus* was mostly absent, and *O. absoloni* occurred in low numbers.

Also the preference area recorded for *Isotoma notabilis* and *Neelus minimus* is supported by other studies. Their abundance was always low in the Swedish pine forest soils. They were, however, fairly abundant in all sites studied by FORSSLUND (1944) (Eu-Pc My, Eu-Pc Dr and Me-Pc At).

5.2.3. Euryecious species (ecological generalists)

Several of the recorded species are well-known generalists, occurring in a wide variety of habitats, also in non-forested sites. Species with such large habitat tolerance are called euryecious or ubiquists. Here we must bear in mind that these species may theoretically be

less euryecious concerning the microenvironments which they inhabit in the soil. In the present paper, the terms are applied to species with a high tolerance for various plant communities and their soils.

On the basis of literature (especially AGRELL 1941, GISIN 1943, STACH 1947, 1949a, b, 1954 and 1957, GISIN 1960, BÖDVARSSON 1961, and FJELLBERG 1980 and pers. comm.), the following ten species have been considered as the most typically ubiquitous species among the 31 species reaching a density of 1,000 per m^2 in my material: *Folsomia quadrioculata s.l.*, *Isotoma notabilis*, *Isotoma viridis*, *Isotomiella minor*, *Lepidocyrtus lignorum*, *Onychiurus armatus s.l.*, *Friesea mirabilis*, *Willemia anophthalma*, *Anurida pygmaea* and *Neelus minimus*.

In four of the seven vegetation types (Va-Pn, Eu-Pc My, Eu-Pc Dr and Me-Pc ty), the dominant species was an ubiquist in both study areas (Table 6).

Several of the *Mesaphorura* species also seem to have a high tolerance for various habitats, including alpine conditions (RUSEK 1971, 1973, 1974 and 1976, PETERSEN 1978b, BENGTSSON & RUNDGREN 1980, FJELLBERG 1980, LIENHARD 1980). Although the ecology of these species is still unsatisfactorily known, the relevant *Mesaphorura* species may prove to belong to the typical ubiquists. In this case, euryecious species will take the two first places on the list in all investigated sites except Cl-Pn and Eu-Pc Dr in area B (Table 6, all *Mesaphorura* species have been underlined). In seven of the fifteen sites, there would be 6—8 ubiquists on the top of the list.

In a study of soil Collembola from twenty different habitats in South Sweden, BÖDVARSSON (1961) found that ubiquists dominated the picture in all but four habitats. These four habitats were characterized by extreme environmental conditions (wet vegetation, dry moss on stones, salt seaweed and dung).

In the present study, fourteen species were found in all the seven vegetation types, when the material from the two study areas is pooled. These species may be considered as the largest ubiquists within coniferous forests in SE-Norway. Ranged after decreasing maximum abundance (given in thousands per m^2 in parentheses after the name), they are: *Isotoma notabilis* (77), *Mesaphorura tenuisensillata* (63), *Isotomiella minor* (58), *Onychiurus armatus s.l.* (33), *Folsomia quadrioculata s.l.* (24), *Friesea mirabilis* (24), *Folsomia sensibilis* (20), *Anurophorus binoculatus* (14), *Lepidocyrtus lignorum* (12), *Willemia anophthalma* (10), *Anurida pygmaea* (9), *Onychiurus absoloni* (9), *Anurida forsslundi* (4), and *Karlstejnia norvegica* (2).

We see that this group of coniferous forest ubiquists contains both abundant and rather scarce species. A high tolerance for various soils is obviously not necessarily coupled with a general high abundance.

Of these fourteen species, I consider *Isotomiella minor* as the largest coniferous forest ubiquist, when quantitative aspects are also taken into consideration. Besides occurring in all samplings, its abundance was rather high in all sites except for the two poorest vegetation types. Furthermore, its constancy values were high; in most sites the species occurred in all or nearly all soil cores. In area B, it was the dominant species in all sites except the two poorest soils. In FORSSLUND's (1944) material, *I. minor* was the most common species in all investigated habitats (Eu-Pc My, Eu-Pc Dr and Me-Pc At).

5.2.4. Stenoecious species (ecological specialists)

Among the species listed in Table 6, some occurred mainly in one or a few vegetation types. Here their numbers might be considerable, as *Isotoma olivacea* in Me-Pc At (area A and B), *Xenylla boerneri* in Cl-Pn (area B) and *Anurophorus septentrionalis* in Cl-Pn and Ba-Pn (area A). Such species were found mainly in the very dry or the very moist sites, and literature data confirm that these are "ecological specialists" (stenoecious species). Hygrophilic species are surrounded by an unbroken frame in Table 6, and xerophilic species by a broken frame.

Isotoma olivacea is a typical hygrophilic species, occurring mainly in very wet soils (FJELLBERG 1974b, 1979, 1980). Both soils where it occurred abundantly in the present study were moist, often under the influence of seeping water.

Table 6. List of species reaching abundance values above 1,000 ind. m^{-2} in each habitat, ranged

STUDY AREA A

Cl-Pn	Ba-Pn	Va-Pn	Eu-Pc My	Eu-Pc Dr	Me-Pc Dy	Me-Pc At A_1	Me-Pc At A_2
Mesaphorura tenuisensillata 63.4	ONYCHIURUS ARMATUS S.L. 13.9	FOLSOMIA QUADRIOCULATA S.L. 23.6	ONYCHIURUS ARMATUS S.L. 32.7	ISOTOMIELLA MINOR 18.7	ISOTOMA NOTABILIS 77.3	ISOTOMIELLA MINOR 45.7	Mesaphorura sylvatica 26.4
ONYCHIURUS ARMATUS S.L. 16.2	Mesaphorura tenuisensillata 11.1	ONYCHIURUS ARMATUS S.L. 15.8	ISOTOMIELLA MINOR 13.3	ISOTOMA NOTABILIS 17.3	FRIESEA MIRABILIS 23.9	ISOTOMA NOTABILIS 14.0	ISOTOMA NOTABILIS 13.3
Anurophorus septentrionalis 13.2	LEPIDOCYRTUS LIGNORUM 6.4	Mesaphorura tenuisensillata 10.9	LEPIDOCYRTUS LIGNORUM 12.2	ONYCHIURUS ARMATUS S.L. 10.6	FOLSOMIA QUADRIOCULATA S.L. 20.6	Mesaphorura tenuisensillata 9.0	Isotoma olivacea 11.6
FOLSOMIA QUADRIOCULATA S.L. 10.4	FRIESEA MIRABILIS 6.0	Mesaphorura macrochaeta 9.1	Mesaphorura yosii 11.9	Isotoma hiemalis 9.9	ONYCHIURUS ARMATUS S.L. 19.2	ONYCHIURUS ARMATUS S.L. 8.3	Mesaphorura macrochaeta 9.9
FRIESEA MIRABILIS 6.4	Anurophorus septentrionalis 5.4	ANURIDA PYGMAEA 9.0	Mesaphorura tenuisensillata 8.3	FOLSOMIA QUADRIOCULATA S.L. 9.6	ISOTOMIELLA MINOR 16.1	NEELUS MINIMUS 4.4	ISOTOMIELLA MINOR 9.8
Isotoma sensibilis 3.2	Anurida forsslundi 3.7	ISOTOMIELLA MINOR 8.7	ISOTOMA NOTABILIS 7.2	ANURIDA PYGMAEA 6.8	Mesaphorura sylvatica 12.3	Mesaphorura macrochaeta 3.9	Mesaphorura tenuisensillata 6.0
LEPIDOCYRTUS LIGNORUM 1.9	Mesaphorura yosii 2.4	Mesaphorura yosii 5.7	ANURIDA PYGMAEA 6.5	Mesaphorura sylvatica 6.4	Lepidocyrtus cyaneus 12.2	LEPIDOCYRTUS LIGNORUM 3.0	ONYCHIURUS ARMATUS S.L. 4.2
Hypogastrura inermis 1.3	Isotoma olivacea 2.4	Mesaphorura sylvatica 4.2	FOLSOMIA QUADRIOCULATA S.L. 5.5	Mesaphorura tenuisensillata 3.9	Mesaphorura tenuisensillata 9.9	Anurophorus binoculatus 2.4	NEELUS MINIMUS 3.7
ISOTOMIELLA MINOR 1.1	ANURIDA PYGMAEA 2.0	Anurida forsslundi 3.6	Lepidocyrtus cyaneus 4.2	FRIESEA MIRABILIS 3.8	LEPIDOCYRTUS LIGNORUM 6.3	Willemia aspinata 1.8	FOLSOMIA QUADRIOCULATA S.L. 3.2
Anurida forsslundi 1.1	Sminthuridae spp. juv. 1.2	FRIESEA MIRABILIS 2.6	FRIESEA MIRABILIS 3.5	LEPIDOCYRTUS LIGNORUM 1.8	Sminthuridae spp. juv. 5.8	Wankeliella mediochaeta 1.4	LEPIDOCYRTUS LIGNORUM 2.0
		Tullbergia callipygos 2.3	Karlstejnia norvegica 2.1	NEELUS MINIMUS 1.0	ISOTOMA VIRIDIS 5.5	FOLSOMIA QUADRIOCULATA S.L. 1.3	FRIESEA MIRABILIS 1.7
		Hypogastrura inermis 1.6	WILLEMIA ANOPHTHALMA 1.7		Sminthurinus aureus 2.9	Mesaphorura sylvatica 1.1	
		LEPIDOCYRTUS LIGNORUM 1.6	Folsomia sensibilis 1.3		Anurida forsslundi 1.9	Arrhopalites sp. juv. 1.1	
		Karlstejnia norvegica 1.0			Karlstejnia norvegica 1.8	Sminthuridae spp. juv. 1.0	
					ANURIDA PYGMAEA 1.8		
					NEELUS MINIMUS 1.6		
					Mesaphorura yosii 1.5		
					Isotoma hiemalis 1.4		
					Mesaphorura macrochaeta 1.2		

Four xerophilic species are characteristic for the pine forest sites: *Xenylla boerneri*, *Isotoma sensibilis*, *Hypogastrura inermis* and *Anurophorus septentrionalis* (Table 6). The first two occur either in dry litter or in dry and exposed habitats, such as behind loose bark or in the thin layer of moss and lichens on stones, cliffs and tree trunks (AGRELL 1941, GISIN 1943 and 1960, STACH 1947 and 1949a, BÖDVARSSON 1961, FJELLBERG 1980). Evidently *X. boerneri* may be highly aggregated on favourable microsites, as the majority of animals were found in one sample (0—3 cm), which ontained 375 specimens and no individuals of other species. *H. inermis* occurs mainly in dry needle litter, especially of pine, but may also be found below old bark (LINNANIEMI 1912, AGRELL 1941, GISIN 1943, STACH 1949a, AXELSSON *et al.* 1973, WIRÉN 1975, BÅÅTH *et al.* 1980, and FJELLBERG 1980). Recent, correct identifications of *A. septentrionalis* show that it is a typical inhabitant of dry coniferous litter, especially pine litter (PERSSON 1975, WIRÉN 1975, BÅÅTH *et al.* 1980, FJELLBERG 1980, LEINAAS pers. comm., HÅGVAR unpubl.). Of the four species, this is perhaps the least xerophilic. From Table 6 it appears that it was fairly abundant also in the Ba-Pn habitat in area A. Here, the soil was periodically rather moist, and we observe that the hygrophilic species *Isotoma olivacea* was

after the highest abundance noted for each species.[1])

STUDY AREA **B**

Cl-Pn	Ba-Pn	Va-Pn	Eu-Pc My	Eu-Pc Dr	Me-Pc ty	Me-Pc At	SYMBOLS
Xenylla boerneri 21.5	Mesaphorura yosii 18.5	ISOTOMIELLA MINOR 24.5	ISOTOMIELLA MINOR 21.2	ISOTOMIELLA MINOR 57.9	ISOTOMIELLA MINOR 21.1	ISOTOMIELLA MINOR 24.3	LARGE LETTERS: EURYECIOUS SPECIES (UBIQUISTS)
FOLSOMIA QUADRIOCULATA S.L. 12.4	FOLSOMIA QUADRIOCULATA S.L. 9.3	FOLSOMIA QUADRIOCULATA S.L. 17.1	FOLSOMIA QUADRIOCULATA S.L. 16.5	Folsomia sensibilis 19.5	Mesaphorura tenuisensillata 13.9	ISOTOMA NOTABILIS 19.0	
Mesaphorura tenuisensillata 9.6	ISOTOMIELLA MINOR 7.7	ONYCHIURUS ARMATUS S.L. 15.7	Anurophorus binoculatus 14.4	Mesaphorura yosii 17.9	Mesaphorura italica 10.9	Isotoma olivacea 18.9	
FRIESEA MIRABILIS 6.5	FRIESEA MIRABILIS 6.8	Mesaphorura yosii 11.4	FRIESEA MIRABILIS 13.0	Mesaphorura tenuisensillata 10.6	ISOTOMA NOTABILIS 6.6	Mesaphorura tenuisensillata 5.6	
ISOTOMIELLA MINOR 2.4	Mesaphorura tenuisensillata 6.6	FRIESEA MIRABILIS 6.2	Mesaphorura yosii 12.1	Anurophorus binoculatus 9.6	ONYCHIURUS ARMATUS S.L. 6.3	FOLSOMIA QUADRIOCULATA S.L. 2.2	SPECIES WITH UNBROKEN FRAME: HYGROPHILIC
Mesaphorura yosii 1.9	WILLEMIA ANOPHTHALMA 5.7	Mesaphorura tenuisensillata 4.6	WILLEMIA ANOPHTHALMA 9.9	Onychiurus absoloni 8.5	Mesaphorura cf. sylvatica 5.9	FRIESEA MIRABILIS 2.0	
LEPIDOCYRTUS LIGNORUM 1.1	Anurophorus binoculatus 3.8	Anurophorus binoculatus 3.1	ISOTOMA NOTABILIS 7.4	Mesaphorura sylvatica 7.7	Mesaphorura sylvatica 5.5	ONYCHIURUS ARMATUS S.L. 1.5	
	Folsomia sensibilis 3.4	Anurida forssłundi 2.4	Onychiurus absoloni 4.6	WILLEMIA ANOPHTHALMA 7.4	FRIESEA MIRABILIS 5.4	NEELUS MINIMUS 1.4	SPECIES WITH BROKEN FRAME: XEROPHILIC
	ANURIDA PYGMAEA 2.6	ANURIDA PYGMAEA 1.5	Mesaphorura tenuisensillata 4.5	ISOTOMA NOTABILIS 6.5	Folsomia sensibilis 4.0	Sminthuridae spp. juv. 1.2	
	ISOTOMA NOTABILIS 2.5	Mesaphorura sylvatica 1.1	ONYCHIURUS ARMATUS S.L. 4.3	FRIESEA MIRABILIS 6.2	ISOTOMA VIRIDIS 3.9	Tullbergia quadrispina 1.1	
	ONYCHIURUS ARMATUS S.L. 1.7		Folsomia sensibilis 4.1	ONYCHIURUS ARMATUS S.L. 3.5	Willemia aspinata 2.6		Mesaphorura – SPECIES ARE UNDERLINED
	Onychiurus absoloni 1.6		Isotoma olivacea 2.8	ANURIDA PYGMAEA 2.0	FOLSOMIA QUADRIOCULATA S.L. 2.1		
	LEPIDOCYRTUS LIGNORUM 1.6		ANURIDA PYGMAEA 2.4	Anurida forssłundi 1.1	Onychiurus absoloni 1.3		
	Isotoma olivacea 1.1		Karlstejnia norvegica 1.6	LEPIDOCYRTUS LIGNORUM 1.0			FIGURES INDICATE THE HIGHEST ABUNDANCE OBSERVED, IN THOUSANDS PER M^2
			Willemia aspinata 1.3				
			Mesaphorura italica 1.2				

[1]) The ten most typical ubiquists, written in large letters in the table' dominate the fauna strongly in most habitats.

number eight on the ranking list. This site probably contains both dry and moist microhabitats, since the two species were never abundant in the same soil sample. The species were also fairly well separated vertically, *A. septentrionalis* occurring mainly in the 0—3 cm layer and *I. olivacea* in the 3—6 cm layer.

The importance of soil moisture for single species as well as the structure of the Collembola communities has been stressed by several workers. For instance, AGRELL (1941) noted a large similarity in the Collembola fauna of various moist alpine habitats, and, correspondingly, a large similarity between various dry habitats. In tundra soils on Spitsbergen, SENDSTAD (1977) found characteristic species for various moist habitats, and other characteristic species for different dry habitats.

At this stage, I do not find it fruitful to discuss the possible existence of other "indicator species" in the material other than the xerophilic/hygrophilic elements. We may, however, conclude that the different vegetation types, each characterized by the presence of certain plant species mirroring soil quality, do not contain equally good series of indicator species among Collembola.

5.2.5. Pairs of species

Two species having closely similar distribution patterns on the various vegetation types and soils must either have similar niches, or different niches occurring in the same sites. A very broad niche in both species, including a tolerance for all the relevant habitats, is a special case of the first alternative. In the second alternative, two species may, for instance, prefer various decomposition stages of the same litter type, or prefer different litter types from the same plant species. Thus, a high similarity index, even on a quantitative basis (SPATZ' index), only implies that there is a good chance of obtaining the two species in similar numbers in a given soil core. The species may, for instance, have different vertical distributions. This is the case for the two pairs which achieved the highest values of SPATZ' index: *Mesaphorura tenuisensillata* together with either *Friesea mirabilis* or *Onychiurus armatus s.l.* As an example, *F. mirabilis* occurred mainly in the 0—3 cm layer in the Va-Pn habitat in area A, while *M. tenuisensillata* mainly lived in the 3—6 cm layer, and *O. armatus s.l.* was common in both layers.

Furthermore, the similarity indexes between species are only valid for the relevant range of habitats, in this case the different types of Norwegian coniferous forests. Species which behave similarly in coniferous forest may very well reveal profound differences in habitat choice if other types of nature are included, as alpine areas, bogs, sea shores, etc. Conversely, species may be better correlated in habitats other than in coniferous forest.

BÖDVARSSON's (1961) work on Collembola from very different habitats in South Sweden may illustrate this situation. He made similarity indexes between the twelve species with highest frequencies, calculating the number of samples in which both species occurred in per cent of the samples containing at least one of the species. The principle is similar to SÖRENSEN's index in the present study. While *Isotomiella minor* and *Onychiurus armatus s.l.* achieved the maximum index of similarity by SÖRENSEN's method in the present study, the species were to a large degree separated in BÖDVARSSON's study. *Isotoma notabilis* together with *Folsomia quadrioculata s.l.* or *Onychiurus armatus s.l.* were two pairs having some of the highest indexes in the Swedish study, while these pairs were not ranged so high in the present study.

It is remarkable that all high indexes in the present study were between coniferous forest ubiquists. This indicates that most of the non-ubiquists have rather different preferences or tolerances. Fig. 9, showing the main range for each of the common species along the soil fertility gradient, also illustrates this segregation. The species do not occur in clusters, each concentrated around one or a few vegetation types. Evidently there is no "barrier" between podzol and brown earth soils, as many species extend their main range into both soil types.

5.3. Relations between plant and Collembola communities

The Collembola fauna proved to be so different in the two study areas that many communities showed greatest similarity to another community within the same study area. In fact, only 33 of the 60 Collembola species were found in both areas. A similar picture appeared for the plant communities when all species, not only the "indicator species" for the vegetation types, were taken into consideration. These differences between the two study areas may be related to climate, geology or other factors.

However, in spite of this, the fauna in the poorest (Cl-Pn) and the richest (Me-Pc At) soils very often showed greatest similarity to the corresponding habitat in the other study are. In quantitative terms, there was also a high floristic similarity between the two study areas at the ends of the soil fertility scale. These relations may to a large degree be due to soil moisture conditions. Cl-Pn was the driest habitat, while Me-Pc At had the highest soil moisture.

Another conclusions which can be drawn from the total material is that natural groupings of the Collembola communities are related to soil fertility (Figs. 11 and 12). Even if each group tends to be dominated by communities from one area, the various groups reflect different sections of the soil fertility gradient.

The observation that local characteristics of the Collembola fauna may mask effects of vegetation and soil is supported by other studies. FORSSLUND (1944) studied the microarthropod fauna in two closely situated coniferous forest sites in Northern Sweden. Even with similar vegetation types in the two areas (Eu-Pc My, Eu-Pc Dr and Me-Pc At), the differences between the two study areas were more striking than between the vegetation types. A very typical ubiquistic (euryecious) Collembolan, *Onychiurus armatus s.l.*, was quite absent in one area. Another ubiquist, *Folsomia quadrioculata s.l.*, proved to be absent from both his study areas.

Other studies have shown the absence of these two ubiquitous species from certain coniferous forest localities without any apparent environmental reason. Both species were absent from a pine forest locality studied by PERSSON (1975). In certain other pine localities in Sweden (WIRÉN 1975, LOHM *et al.* 1977, BÅÅTH *et al.* 1980), one or both were either absent or sometimes present in considerable numbers. *F. quadrioculata s.l.* was also absent from a Norwegian spruce forest (Eu-Pc My) studied by LEINAAS (1976).

Absence of a species from a site which should be ecologically acceptable might be due to competition, or simply to recent immigration or a low colonising rate. The relatively short time since the last glaciation may imply that some species have not yet colonised all potential habitats.

The most fruitful comparison between plant and Collembola communities appeared when only sites within each study area were compared. When the plant communities were ranged according to soil fertility, neighbouring plant communities very often had similar Collembola communities. In one case, these relations were as good as possible, and they were always better than random (Fig. 14). Apparently, both species composition and the quantitative composition of the Collembola fauna are to a large degree correlated with soil fertility, expressed through vegetation types.

Deviations from this pattern, i.e. high similarity indexes between non-neighbouring vegetation types were in certain cases supported by corresponding floristic connections. Again, soil humidity may have been a decisive factor for both Collembola and plants. For instance, both Eu-Pc Dr and Me-Pc At have a moist soil, while Me-Pc ty has a drier soil and in this respect has a closer connection to Eu-Pc My than to any "neighbouring" vegetation type.

In four neighbouring vegetation types in area B (Ba-Pn, Va-Pn, Eu-Pc My and Eu-Pc Dr), the soil profile was very similar, with an iron podzol profile (Typic Udipsamment) containing a well-developed bleached layer (E). Especially in the autumn, the Collembola fauna proved to be very similar in these habitats. The similarity was most pronounced regarding species composition.

The habitat containing a Collembola fauna most different from all other sites was Ba-Pn in area A. This was probably due to very special soil conditions, as this habitat was the only one containing a peat soil. Otherwise, the lowest similarity indexes were between the poorest and richest soils.

Besides the geographical position of the habitats, the Collembola communities are probably regulated by a number of factors. Soil fertility, soil profile, humus type and water content may be important, but other factors, such as microflora, pore volume, etc., may certainly also influence their life conditions. When we add climatic factors to this list, it is not surprising that vegetation is only partially correlated with a certain group of soil organisms.

In his survey of Collembola, CHRISTIANSEN (1964) summed up the connection between macroflora and Collembola by saying that there is generally a moderate amount of correspondance between plant and Collembolan associations, but little evidence of restriction of individual Collembola species to one species of plant. BELLINGER (1954) had earlier reached similar conclusions.

A parallel situation seems to exist for Oribatei. WAUTHY & LEBRUN (1980) studied the Oribatei communities of deciduous forests in Belgium and found a low correlation with the vegetation communities. They concluded that the deciduous phytocenoses were mainly influenced by climatic factors, while the taxocenoses of Oribatei which they shelter are primarily regulated by the edaphic factors and, secondarily, by climatic factors.

Haarløv (1960) found large similarities in the microarthropod fauna of different Danish vegetation types and soils, and largest similarities between either the very dry or the very moist sites. Supported by Tuxen's (1944) study of the fauna of the hot springs of Iceland, he stressed the limited rate of spreading of microarthropoda and stated that the Collembola and Acari fauna of a given habitat will largely be recruited from the nearest surroundings.

In a study of Collembola in various forest types in Poland, including both deciduous and coniferous trees, Szeptycki (1967) concluded that their fauna was "astonishing alike". The relevant sites differed in soil, inclination, exposition, microclimate, etc. He considered that the main factor regulating the Collembola fauna in these forests was the presence of conifers, which give a litter with special chemical features.

Wallwork (1970) has concluded that the Collembola fauna of a certain locality is determined by a complex of factors, both ecological and historical. Therefore, he considered that the degree of similarity in species composition between two sites can be used as an index of an overall ecological similarity. He further suggested that the influence of vegetation types is an indirect one, being exerted, perhaps, through its effect on soil type, microfloral composition, or soil moisture.

A better insight into Collembola ecology is needed before the distribution of communities can be properly explained. However, up to this point, it seems that the more extreme the environmental conditions are (e.g. soil moisture), the better can vegetation indicate the Collembola fauna.

5.4. Comparisons with the Enchytraeidae fauna in corresponding vegetation types

A study parallel to the present has been performed for Enchytraeidae (Abrahamsen 1972). The study was made in corresponding vegetation types, and some of the sampling sites were identical to the present ones. In addition, the enchytraeid study included a third locality in Southern Norway. It is interesting to compare some of the main conclusions in the two studies, as both Collembola and Enchytraeidae are abundant representatives of the soil fauna in coniferous forests.

The number of enchytraeid species also increased with increasing soil fertility. However, the increase was stronger and more concentrated to the richest soils than in Collembola. Species numbers were very low in the poorest soils (2—7 species in the range Cl-Pn — Eu-Pc Dr). In Me-Pc ty habitats, 7—11 species were found, and as much as 15—21 in the richest soils (Me-Pc At).

Total abundance of Enchytraeidae was generally lower than for Collembola, the maximum values being about 85,000 m^{-2} (Eu-Pc My habitat). Most values were between 20,000 and 50,000 m^{-2}. While the highest numbers of Collembola were observed on the Eu-Pc Dr/Me-Pc ty level, the highest abundance values of Enchytraeidae were found in Eu-Pc My in two areas and in Cl-Pn in the third area.

Also among Enchytraeidae were species preferring different sections of the soil fertility gradient. A large fraction of the species were, however, characteristic for the richest soil.

As in Collembola, there was only a moderate correlation between vegetation and animal communities. Within the two highest fertility levels, there was a rather good faunistic correlation between sites with corresponding vegetation type in different areas. However, enchytraeid communities in poorer soils often showed highest similarity with another vegetation type in a different study area.

6. Acknowledgements

I am greatly indebted to A. Fjellberg, who kindly identified several difficult species, and to J. Rusek for checking the identifications of the *Mesaphorura* spcies. I will also express my gratitude to G. Abrahamsen for selecting most of the sampling sites and for critical reading of the manuscript, to T. Amundsen for doing the main work with the vegetation analysis, to K. Bjor for critical reading of the manuscript, to A. Hjeltnes for help with the statistical calculations, to H. Korsmo for selecting two of the sampling sites, to H. P. Leinaas for various valuable advice, and to A. Stuanes for help with soil descriptions. Mrs. L. Hjeljord kindly improved the English. This in SNSF-contribution FA 128/81.

7. Résumé

(Les collemboles des sols de forêts de conifères, relations avec les communautés végétales et la fertilité du sol)

La faune des Collemboles édaphiques a été étudiée dans deux domaines de forêts de conifères du sud-est de la Norvège. Dans chaque domaine sept types de végétation ont été retenus selon différents niveaux de fertilité du sol. Les trois sols les plus pauvres se situent dans les forêts de pin *(Pinus sylvestris)*, tandis que les quatre sols les plus riches se trouvent dans les forêts de sapin *(Picea abies)*. La collecte des Collemboles a été effectuée durant le printemps et l'automne. Les résultats obtenus sont présentés ci-après.

(1) Au total 60 espèces ont été répertoriées. Dans toutes les situations la plupart des espèces sont rares (46 % en moyenne) avec des valeurs de dominance inférieures à 1 %. Dans la plupart des sols la faune est quantitativement dominée par un petit nombre de «généralistes» écologiques. Cependant, dans le sol le plus pauvre, étant en outre le plus sec, les espèces résistantes à la sécheresse sont abondantes. Dans le sol le plus riche, qui possède d'ailleurs la teneur la plus élevée en eau, une espèce hygrophile est particulièrement dominante.

(2) Dans les deux domaines étudiés, on a observé les caractéristiques suivantes:
   a. Le nombre d'espèces récoltées augmente: environ 20 espèces dans le sol le plus pauvre jusqu'à 30 dans le sol le plus riche.
   b. L'abondance par m² augmente: environ 50000 individus dans le sol le plus pauvre, autour de 100000 dans les sols de deuxième et troisième niveau de richesse, environ 70000 dans le sol le plus riche.
   c. L'indice de diversité (H') de Shannon-Wiener est le plus élevé dans les sols moyennement riches. La proportion d'espèces rares y est également la plus basse.

(3) Trois espèces sont courantes dans tous les types de sol. Les autres espèces se trouvent principalement dans un domaine limité du gradient de fertilité, mais dans des proportions différentes selon les espèces. Les tendances principales des différentes espèces sont assez bien réparties selon le gradient de fertilité. Chacune des espèces les plus courantes ont l'abondance la plus élevée dans les types de végétation similaire quelle que soit l'aire étudiée.

(4) Parmi les espèces d'abondance supérieure à 1000 individus par m², toutes les paires possibles d'espèces ont été testées quant à leur occurence et leur abondance dans divers types de végétation. Les index de similarité les plus élevés ont été trouvés pour les espèces «généralisatrices» présentes fréquemment tout au long du gradient.

(5) La faune des Collemboles dans les deux aires étudiées est différente à plusieurs points de vue. Seulement 33 du total des 60 espèces ont été trouvées dans les deux domaines, mais il s'agit pour la plupart des espèces courantes.

(6) Par suite du caractère «local» de la faune, la similarité des communautés de Collemboles est souvent plus grande entre les sols différents d'un même domaine, qu'entre les sols et les types de végétation analogues des deux domaines. Cependant, les communautés de Collemboles du sol le plus pauvre et du sol le plus riche sont généralement les plus similaires à la communauté du même type de sol dans l'autre domaine. Dans le même domaine, les types de sol très proches sur le plan de la fertilité (d'après les types de végétation) montrent une similitude élevée quant aux communautés de Collemboles.

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Synopsis: *Original scientific paper*
HÅGVAR, S., 1982. Collembola in Norwegian coniferous forest soils. I. Relations to plant communities and soil fertility. Pedobiologia **24**, 255—296.

In each of two coniferous forest sites in SE-Norway, the soil-living Collembola fauna was investigated in seven different vegetation types. Soils ranged from poor podzol soils to rich brown earth. A total of 60 Collembola species were found. In all sites, a large fraction of the species (mean value 46 %) were rare, with dominance values below 1 %. In most soils, the fauna was quantitatively dominated by a few euryecious species (ecological generalists).

Species numbers increased with increasing soil fertility. Total abundance was highest in the second or third richest soils, while diversity was highest in medium rich soils.

Three species were common in all vegetation types. The main ranges of the other species varied greatly, but could in most cases be related to soil fertility. All vegetation types favoured some species.

Within each study area, soils near each other on the fertility scale (according to the vegetation types) showed a high similarity in the Collembola communities. However, due to differences in species composition between the two study areas, corresponding vegetation types might contain rather different Collembola communities. It is suggested that the more extreme the environmental conditions are (e.g. soil moisture), the better can vegetation indicate the Collembola fauna.

Key words: Collembola, coniferous forest, plant communities, soil fertility, species pairs, community similarity.